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Host-parasite relationships of five species of cyclocoelids (Trematoda: Cyclocoelidae)

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HOST-PARASITE RELATIONSHIPS OF FIVE SPECIES OF CYCLOCOELIDS (TREMATODA: CYCLOCOELIDAE)

by

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INTRODUCTION

Trematodes of the family Cyclocoelidae parasitize principally avian respiratory systems. Gravid worms lack an acetabulum and have two intestinal crura which are confluent posteriorly. No sporocyst stage occurs in the life cycle; the cercarial stage is tailless.

Each egg released by a gravid cyclocoelid contains a miracidium enclosing a rediae. Intermediate hosts of cyclocoelid are either terrestial or aquatic snails. In life cycles involving terrestial intermediate hosts, the egg is passively ingested; in cycles involving aquatic molluscs, the miracidium hatches, and its enclosed redia actively penetrates the snail host. In known life cycles of cyclocoelids, only a single molluscan intermediate host occurs. Regardless of the species of intermediate host, the redia leaves the miracidium and bores into the internal organs of the snail. Subsequent development within the snail may follow one of two pathways, depending upon the species of cyclocoelid. Germinal masses within the redia may produce cercariae which encyst within the same redia, or germinal masses may produce cercariae which leave the redia and encyst within the snail's tissues. Birds become infected by eating snails containing mature metacercariae.

I studied the larval development of several species, including: Cyclocoelum brasilianum Stossich, 1902, from

Greater Yellowlegs (Totanus melanoleucus) and Lesser Yellowlegs (Totanus flavipes); Cyclocoelum obscurum Leidy, 1887, recovered from Wilson's Snipe (Capella gallinago); and Cyclocoelum vanelli Rudolphi, 1819, which parasitizes American Avocets (Recurvirostra americana). Also reported herein is the complete life history of Cyclocoelum oculeum Kossack, 1911, in American Coots (Fulica americana). I also attempted to determine the early larval development of Cyclocoelum tringae Stossich, 1902, from the Pectoral Sandpiper (Erolia melanotos). This dissertation includes, in addition, data on the incidence of cyclocoelids in their avian hosts.

HISTORICAL REVIEW

Trematodes of the family Cyclocoelidae have been the subject of much taxonomic controversy and confusion. The systematics of this group has been revised by numerous authors (Brandes, 1892; Looss, 1902; Stossich, 1902; Kossack, 1911; Harrah, 1922; Witenberg, 1923, 1926; Joyeux and Baer, 1927; Dollfus, 1948; Yamaguti, 1958; and Dubois, 1959). Dubois' (1959) revision of the family included two subfamilies, Cyclocoelinae with two genera, Cyclocoelum and Ophthalmophagus, and Typhlocoelinae with two genera, Typhlocoelum and Neiviia. According to Dubois (1959) the genus Cyclocoelum includes three subgenera (Cyclocoelum, Haematotrephus, and Hyptiasmus) and 23 species.

Wootton (1964) felt that Dubois' classification was too restrictive and that the subgenera proposed by Dubois should be raised to generic level. However, Stunkard (1966) stated that Dubois' (1959) study was a definitive work on the systematics of the family. The latter's classification is followed, although I do not agree with his subgeneric classification.

The life cycle of Typhlocoelum sisowi (=Tracheophilus sisowi), a duck parasite, was the first cyclocoelid life history to be reported (Szidat, 1932, 1933). Its pattern includes a miracidium containing a redia which hatches from the egg and attaches to a snail. The redia penetrates the snail leaving

the miracidium behind and comes to lie in the visceral mass near the albumin gland. Eight to 10 days later, germinal masses and cercariae are present within the redia. The cercariae, each of which possesses a penetration organ, an acetabulum, unicellular glands and a digestive tract, eventually escape via the birth pore of the redia and encyst within the snail. Here they develop into metacercariae and must be eaten by the definitive host to complete the cycle. After such ingestion, metacercariae excyst in the small intestine and migrate to the bird host's respiratory passages. Szidat (1933) was unable to determine whether larval cyclocoelids migrate to the bird's lungs by way of the coelomic cavity or via the blood vessels. Six weeks were required for the trematodes to reach sexual maturity.

Stunkard (1934) studied the same trematode Typhlocoelum sisowi (=Typhlocoelum cymbium) recovered from the Pied-Billed Grebe (Podilymbus podiceps) and traced its development through the metacercarial stage in the snail Helisoma trivolvis. He was unable to recover adults 12 weeks after having fed metacercariae to a domestic duck.

Johnston and Simpson (1940) found Cyclocoelum jaenschi in two species of grebes (P. poliocephalus and P. novaehollandiae). They observed that its development through the metacercarial stage in the snail (Ameria sp.) was similar to that in T. sisowi.

Ginetzinskaja (1949), while studying Cyclocoelum mutabile (=Cyclocoelum microstomum), fed metacercariae from laboratory-

reared snails (Lymnaea ovata) to European Coots (Fulica atra). Eighteen hours later, young C. mutabile were found in the bird's blood stream and liver. After feeding on parenchyma cells in the liver, the young trematodes migrated to the air sacs near the heart and dorsal aorta. Later, Ginetzinskaja (1952) discussed larval development of this trematode in L. ovata. She indicated that metacercariae were found usually in the snail's foot near the eye and redula. Ginetzinskaja (1954) completed her investigations on the biology of C. mutabile and found its life cycle to be similar to that of T. sisowi.

Ingersoll (1954) studied C. mutabile (=C. microstomum) from American Coots (Fulica americana). He found that five species of snails representing five genera (Lymnaea stagnalis, Stagnicola palustris, Menetus exacuous, Physa gyrina, and Gyraulus sp.) and two species of avian definitive hosts, American Coots and the Sora Rail (Porzana carolina), could be experimentally infected with C. mutabile.

Timon-David (1950) described a cyclocoelid, Cyclocoelum elongatum (=Cyclocoelum dollfusi), from the air sacs of the Black-Billed Magpie (Pica pica) and reported its life cycle in 1955. This life history differs from those of T. sisowi, C. jaenschi, and C. mutabile in at least three ways, namely: the intermediate host is a land snail (Helicopis arenosa) rather than an aquatic gastropod, eggs containing miracidia are ingested passively by the snail, and cercariae encyst within the rediae producing them.

More recently, Palm (1963) reported Cyclocoelum oculeum (=Trancoelum oculeum) from the nasal cavities and orbits of the European Coot. Larval development in this species, according to him, was the same as in other species mentioned except for C. elongatum.

Wootton (1964) also studied Cyclocoelum oculeum (=Cyclocoelum californicum) from the orbits and nasal cavities, and C. mutabile from the air sacs of the American Coot. He recovered metacercariae of C. oculeum and C. mutabile from Physa gyrina. However, Wootton was unable to infect domestic ducks and chickens with these metacercariae.

MATERIALS AND METHODS

Coots, ducks, and shorebirds were collected from various marshes, lakes, and streams in Iowa and South Dakota. Birds were brought back to the laboratory and examined immediately for trematodes. Each host was opened by making an incision from the vent to the pectoral girdle; the digestive tract, liver, kidneys, lungs, trachea, bursa of Fabricius, and beak were removed and placed in separate containers of avian saline. Each organ was examined under a dissecting microscope for the presence of cyclocoelids. Carcasses of necropsied birds were soaked in saline for several hours to aid in recovery of any remaining trematodes. Finally, the orbits, beak and body cavity were flushed with a strong stream of distilled water to dislodge any remaining cyclocoelids.

Cyclocoelid eggs were collected after their release by adults, or after adult worms had been teased apart in previously boiled aquarium water. Miracidia hatching from these eggs were placed in a drop of dilute methyl cellulose on a microscope slide and were stained with neutral red or Nile blue sulfate prior to study under a compound microscope. Living specimens were measured with the aid of an ocular micrometer or by using photomicrographs of a stage micrometer and photomicrographs of larval stages at the same magnification. The silver nitrate technique of Lynch (1933) was used to stain epidermal plate boundaries of miracidia.

Gravid cyclocoelids that had released their eggs, and immature trematodes were fixed without coverslip pressure in AFA, Bouin's or Zenker's fluid. AFA fixed specimens were transferred to 70% ethanol, stained in either Mayer's paracarmine, counterstained in fast green, or stained in Ehrlich's haematoxylin. Specimens were cleared in methyl salicylate and mounted in synthetic resin (Permount). Cyclocoelids to be sectioned were fixed in either Bouin's or Zenker's fluid. Sections were cut at 5 to 10 microns. Those fixed in Bouin's were stained with Heidenhain's iron haematoxylin and counterstained with eosin; specimens fixed in Zenker's were stained with Mallory's triple stain.

Laboratory-reared snails were maintained in artificial spring water. They were fed lettuce, dried maple leaves, and commercial fish food pellets (Glenco Mills; Glenco, Minnesota). Powdered calcium carbonate was added to the water periodically.

Snails were exposed for several hours by placing them in small stender dishes containing miracidia. After exposure, snails were maintained in small aquaria, and at various intervals post-exposure they were either fixed in Zenker's or Bouin's fluids, or were dissected. Fixed snails were sectioned to study migration, pathology, and development within the intermediate host. Larvae taken from snails at various times post-exposure were treated in one of three ways, namely: as living material to be drawn and photographed; as stained

whole-mounts; or as stained sections. Staining methods used for larval whole-mounts and sections were similar to those used for whole-mounts and sections of adult trematodes.

Experimental coots were raised from eggs using the methods of Ingersoll (1954). Experimental Killdeers were raised from eggs or fledglings as recommended by Malone and Proctor (1966). Birds were exposed by feeding them entire or crushed snails containing metacercariae.

Fecal samples of experimentally exposed Killdeers were checked daily for cyclocoelid eggs until the birds were necropsied. Since infected coots release miracidia via external nares when feeding, the drinking water of these hosts was periodically examined for the presence of miracidia.

NATURAL CYCLOCOELID INFECTIONS

During the course of this study, 386 birds of 17 species known to serve as hosts for cyclocoelid trematodes were examined (Table 1). All birds examined were collected in Iowa, except for avocets which were collected in South Dakota. Numerous bird species were examined so that a variety of cyclocoelid species could be obtained for comparative life history studies. Cyclocoelids inhabit various regions of their hosts. Thus, the American Coots (Fulica americana) harbors two species, Cyclocoelum mutabile in the abdominal air sacs and Cyclocoelum oculeum in the orbits and nasal cavities. The Blue-Winged Teal is parasitized by one species of cyclocoelid, Typhlocoelum cucumerinum, in the trachea. Infected shorebirds harbor their respective cyclocoelids in the abdominal air sacs.

Table 1. Birds examined for cyclocoelid infections

Host	Number examined	Number infected	Percent infected
Order Podicipediformes			
Family Podicepidae			
Polilymbus podiceps (Pied-Billed Grebe)	1	0	0

Table 1. (Continued)

Host	Number examined	Number infected	Percent infected
Order Anseriformes			
Family Anatidae			
Anas discors (Blue-Winged Teal)	23	1[a]	4%
Anas carolinensis (Green-Winged Teal)	1	0	0
Order Gruiformes			
Family Rallidae			
Gallinula chloropus (Common Gallinule)	1	0	0
Fulica americana (American Coot)	161	77[b]	48%
Order Charadriiformes			
Family Haematopodidae			
Recurvirostra americana (American Avocet)	5	2[c]	40%
Family Charadriidae			
Pluvialis dominica (American Golden Plover)	1	0	0

[a] *Typhlocoelum cucumerinum*, new host record.

[b] *Cyclocoelum oculeum* and/or *Cyclocoelum mutable*.

[c] *Cyclocoelum vanelli*.

Table 1. (Continued)

Host	Number examined	Number infected	Percent infected
Squatarola squatarola (Black-Bellied Plover)	1	0	0
Charadrius vociferus (Killdeer)	10	0	0
Family Scopolpacidae			
Tringa solitaria (Solitary Sandpiper)	7	0	0
Actitis macularia (Spotted Sandpiper)	11	0	0
Totanus melanoleuscus (Greater Yellowlegs)	22	7[d]	32%
Totanus flavipes (Lesser Yellowlegs)	62	15[d]	24%
Limnodromus scolopaceus (Long-Billed Dowitcher)	11	0	0
Erolia melanotos (Pectoral Sandpiper)	14	2[e]	14%
Erolia minutilla (Least Sandpiper)	15	0	0
Capella gallinago (Wilson's Snipe)	40	3[f]	8%
	386		

[d] *Cyclocoelum brasilianum*.

[e] *Cyclocoelum tringae*.

[f] *Cyclocoelum obscurum*.

Of 161 American Coots, 28 (17%) harbored only C. oculeum, 32 (20%) had only C. mutabile, and 17 (11%) contained both. If single and double infections are totaled, C. oculeum occurred in 45 (28%), and C. mutabile occurred in 49 (31%) of 161 American Coots. The largest number of C. oculeum and C. mutabile per infected bird was nine for the former and 17 for the latter.

Previous reports on the incidence of C. mutabile and C. oculeum show considerable variation. Ingersoll (1954) examined 245 American Coots and found 59 (24%) infected with C. mutabile. Sulgostowska (1958), working in Poland, studied 54 European Coots (Fulica atra) and recovered 1 (1.8%) specimen of C. mutabile. She also examined an unspecified number of Moorhens (Gallinula chloropus) and found one parasitized with three adult C. mutabile in the trachea. Later (1963), Sulgostowska examined 255 European Coots and reported finding one C. oculeum. She stated that only one Redshank (Tringa totanus) harbored three C. mutabile, and that six specimens of this fluke occurred in one of six Gadwalls (Anas strepera). Neither Palm (1963) nor Wootton (1964) mentioned the incidence of C. oculeum in their studies of European and American Coots respectively.

No American investigators including Harrah (1922) have listed incidence of cyclocoelid infections in shorebirds. The present investigation was undertaken in part to increase

our knowledge of cyclocoelids from these hosts. Results of the present study on 199 shorebirds (Charadriiformes) (Table 1) indicates a rather low percentage of cyclocoelid infections from most of these birds.

Several foreign workers have reported data on the incidence of cyclocoelids in shorebirds. Bychowskaja-Pawlowskaja (1953) in Russia reported the following percentages: (1.0%) Lapwings (Vanellus vanellus) with C. mutabile (=C. microstomum); (1.8%) Greenshanks (Tringa nebularia), (9.8%) Wood Sandpipers (T. glareola), (7.0%) Marsh Sandpipers (T. stagnatilis), (3.7%) Black-Tailed Godwits (Limosa limosa), (10.0%) Avocets (Recurvirostra avosetta), and (2.9%) Lapwings with C. obscurum (=C. mutabile); (4.0%) Ruffs (Philomachus pugnax) with C. vanelli (=Uvitellina adelphaga). Unfortunately, the number of birds examined was not given in her paper.

Sulgostowska (1958) reported no cyclocoelids from four Wilson's Snipes (Capella gallinago), three Ruffs, seven Wood Sandpipers, one Spotted Redshank (T. erythropus), and one Red-Backed Sandpiper (Calidris alpina). In a 1963 paper, Sulgostowska stated that one of two Redshanks (T. totanus) was infected with C. mutabile. However, seven Wood Sandpipers, one Common Sandpiper (T. hypoleucos), two Green Sandpipers (T. ochropus), four Wilson's Snipes, one Red-Backed Sandpiper and one Ruff harbored no cyclocoelids.

Macko (1959) checked 258 Ruffs and found 24 (9.3%) to be infected with C. vanelli (=Haematotrephus lanceolatum). In

1960, Macko recovered 51 specimens of C. vanelli from one of three Whimbels (Numenius phaeopus).

Table 2 presents the percentages of Cyclocoelum obscurum infections in seven species of shorebirds examined in Czechoslovakia by Macko (1965b).

Table 2. Birds examined by Macko for cyclocoelids

Host	Number examined	Number infected	Percent infected
T. erythropus	3	1	33.3%
T. totanus	25	6	24.0%
T. nebularia	11	3	27.2%
T. ochropus	8	1	12.5%
T. glareola	72	4	5.5%
L. limosa	15	1	6.6%
Numenius arquata (Curlew)	9	2	22.0%

All studies on cyclocoelid infections in shorebirds, including mine (Table 1), indicate the incidence to be rather low.

LIFE HISTORY OF *CYCLOCOELUM OCULEUM*

Adult *Cyclocoelum oculeum*, parasites of orbits and nasal cavities of American Coots (*Fulica americana*), produce fully developed miracidia which hatch within the trematode's uterus. Miracidia leave via the coot's external nares when it feeds. Released miracidia must attach to suitable snail intermediate hosts or die within 2 hours after hatching. After attachment to the snail's foot, tentacles or mantle collar, the redia contained within the miracidium penetrates the snail. Following penetration, these highly motile rediae are found in various regions of the molluscan host, including the mantle cavity, kidney, albumin gland, or foot musculature. Apparently, rediae do not favor one particular location within the host, since they were seen moving freely from the region of the foot to the albumin gland within *G. hirsutus*.

Four to 6 days post-exposure, germinal masses may be found developing within the redia, and 12 to 14 days after exposure, well-developed cercariae are present. These cercariae leave the redia via a birth pore and encyst as metacercariae within the snail. They may appear in the foot musculature, tentacle, kidney, or albumin gland. The earliest metacercaria seen was within the foot at 17 days post-exposure. Experimentally, *Stagnicola reflexa*, *Physa gyrina*, *Lymnaea stagnalis*, *Gyraulus hirsutus*, and *Helisoma trivolvis* serve as suitable molluscan hosts for *C. oculeum* through the metacercarial stage.

Definitive hosts acquire their infections by ingesting infected snails.

Adult

All gravid specimens of C. oculeum from the orbits and nasal cavities of American Coots (Fulica americana) conform to the description given by Kossack (1911) for C. oculeum (=Hyptiasmus oculeus) recovered from the European Coot (Fulica atra). This parasite has frequently been reported from nasal cavities of rails in Europe and Russia. In the United States, however, only one report, that of Wootton (1964), has appeared in the literature and was based on studies of C. oculeum from nasal cavities and orbits of American Coots collected in northern California. All flukes of this species (Fig. 1) collected for the present study were obtained from coots taken in Iowa lakes and marshes.

Dubois (1959) considered the following as synonyms of Cyclocoelum (Hyptiasmus) oculeum Kossack, 1911:

Hyptiasmus oculeus Kossack, 1911. p. 491-590.
Hyptiasmus oculeus Ivanitzkaja, 1920. p. 1-12.
Transcoelum oculeum Witenberg, 1926. p. 103-186.
Transcoelum sigillum Witenberg, 1926. p. 103-186.
Hyptiasmus (Hyptiasmus) brumpti Dollfus, 1948. p. 129-199.
Hyptiasmus oculeus Ginetzinskaja, 1949. p. 1219-1222.
Hyptiasmus oculeus Bychowskaja-Pawlowskaja, 1953. p. 5-116.
Transcoelum oculeum Palm, 1963. p. 560-567.
Cyclocoelum (Hyptiasmus) californicum Wootton, 1964. p. 524-525.

Egg

Mature eggs of C. oculeum (Fig. 4) are oblong, operculate, and possess fragile transparent shells. Measurements of ten recently shed eggs averaged 0.131 x 0.052 mm.

Within the posterior two-thirds of a gravid fluke's uterus, a complete series of developmental stages may be seen, from immature eggs containing only small miracidial embryos and numerous yolk cells, to larger mature eggs containing fully developed miracidia. In the anterior third of the uterus, actively free-swimming miracidia could be observed. Free-swimming miracidia were found within the uteri of all gravid C. oculeum recovered in the present study.

Gravid adult cyclocoelids release viable miracidia if the adult worms are placed in water. Apparently, coots in nature infected with gravid C. oculeum release miracidia through the external nares when feeding.

Miracidium

Descriptions of miracidia (Fig. 5) are based on observations of living specimens immediately after their emergence from adult trematodes. Data below are based on study of living specimens. Except for studies on epidermal plates, specimens were not fixed and stained for detailed internal anatomical studies.

Externally, C. oculeum miracidia are similar to others described in the family Cyclocoelidae. Measurements of 10

living miracidia averaged 0.192 x 0.069 mm. Cilia are uniform in distribution and length except at the anterior end where they are approximately twice as long as on the rest of the body. The anterior cilia, which resemble a rotating wheel, arise from a collarlike structure surrounding the base of an elongated terebratorium.

Using the silver nitrate technique of Lynch (1933), it was observed that cilia are borne on 21 flattened epidermal plates nearly covering the body except for the terebratorium. The first, second, third, and fourth tiers consist of six, nine, four, and two plates, respectively. This arrangement can be expressed in the formula: 6:9:4:2 (Fig. 3) according to a method suggested by Bennett (1936). This was consistent in 10 specimens of C. oculeum miracidia observed. The only other report of epidermal plates within the Cyclocoelidae was that of Johnston and Simpson (1940), who described 10 epidermal plates arranged in four tiers on one side of a miracidium. They estimated the miracidium to have approximately 15 to 20 plates. Bennett (1936) summarized early work on epidermal plates and reported the following plate patterns for certain families, namely: Paramphistomidae, 6:8:4:2; Strigeidae, 6:8:4:3; Schistosomatidae, 6:8:4:3; Echinostomatidae, 6:6:4:2; Fasciolidae, 6:6:3:4:2; Troglotrematidae, 6:6-7:3:1; and Heronimidae, 4-6:6-10:3-6:1-2.

In addition to epidermal plates, there are small circular bristle-patch plates appearing between the first and second

tiers and between the third and fourth tiers. The specimens I studied did not appear to have a regular arrangement of bristle-patch plates in relation to the epidermal plates. Other studies also indicate that the bristle-patch plate arrangement is not constant. Najim (1956), in a study of miracidia of the avian schistosome Gigantobilharzia huronensis, found bristle-patch plates between the first and second tiers of epidermal plates. However, he never found a consistent arrangement or a constant number of them. Dutt and Srivastava (1961) studied miracidia of six species of mammalian schistosomes and also failed to find a constant pattern or relationship of bristle-patch plates to tiers of epidermal plates.

Internally, C. oculeum miracidia possess a black bilobed eyespot and a fully formed redia (Fig. 5). The redia, located in the posterior two-thirds of the miracidium, possesses two posterior appendages, tail, digestive tract, and a pharynx. This corresponds to Palm's (1963) description of this species. In addition, Palm noted two flame cells within the miracidium; a single pair was also noted in the present study.

Studies on behavior of C. oculeum miracidia indicated that they are positively phototactic and negatively geotactic. When in the vicinity of snails, they do not appear to actively seek out their hosts, but find them by trial and error. When a miracidium contacts a snail, it does not necessarily attach at once, but may move about on the snail's surface

prior to attachment. In many cases, however, it may immediately attach after making contact. Following attachment, the enclosed redia bores into the snail. The length of time for redial penetration is not known for this species.

Snails which could be infected with C. oculeum rediae under experimental conditions include the following: Lymnaea stagnalis, Stagnicola reflexa, Physa gyrina, Helisoma trivolvis, and Gyraulus hirsutus. Palm (1963) was able to infect only Lymnaea ovata of seven genera exposed with C. oculeum rediae and Wootton (1964) infected only Physa gyrina of three genera exposed.

Besides attaching to the snail host, miracidia of C. oculeum have been observed in three instances to attach to the adult cyclocoelid from which they emerged when both were left in the same container. Ingersoll (1954) also noted this behavior in his study of C. mutabile.

Redia

Palm (1963), in his study of C. oculeum rediae, did not include data about larval development in different snails, migrations of larvae within the snail, or their pathological effects. I investigated these areas by studying 147 sectioned and 111 dissected snails, previously exposed to C. oculeum miracidia.

Exposed snails of five species (S. reflexa, H. trivolvis, G. hirsutus, L. stagnalis, and P. gyrina) were dissected, and

sections of the first three named species were also prepared. Redial stages of C. oculeum were recovered from 14 hours to 6 months. Table 3 summarizes these experiments.

First dissections were made 7 days following exposure, but sections were made of exposed snails ranging from those fixed 1 hour to 28 days post-exposure. Not until 14 hours after exposure were rediae observed in sectioned snails. Rediae of this age occurred in connective tissue around the digestive tract as well as in the kidney, foot musculature, and tentacles of S. reflexa and H. trivolvis. Such larvae are fusiform, tailed and possess posterior appendages. Internally, a pharynx, and sacciform intestine surrounded by undifferentiated cells are present, but no evidence of germinal masses could be seen. Such rediae differ little from those observed within the miracidium.

Specimens of sectioned G. hirsutus examined 1, 2, and 3 days post-exposure contained no C. oculeum redia. However, two sectioned specimens of G. hirsutus 4 days after exposure harbored redial infections. One redia occurred in the foot musculature near the snail's digestive tract (Fig. 6). No germinal masses were visible. Within the second C. hirsutus, rediae appeared in connective tissue closely associated with the digestive tract. These rediae possessed developing germinal masses.

Living rediae recovered 7 days post-exposure from connective tissue, mantle cavity, kidney, albumin gland, and

Table 3. Larval development of C. oculeum in molluscan host

Host	Time post-exposure	Germinal masses	Cercariae	Metacercariae
S. reflexa	14 hrs.	Absent	Absent	Absent
H. trivolvis	14 hrs.	Absent	Absent	Absent
G. hirsutus	4 days	Present	Absent	Absent
S. reflexa				
L. stagnalis				
P. gyrina	7 days	Present	Absent	Absent
H. trivolvis				
G. hirsutus				
G. hirsutus	12 days	Present	Present	Absent
S. reflexa				
L. stagnalis				
P. gyrina	14 days	Present	Present	Absent
H. trivolvis				
G. hirsutus				
G. hirsutus	17, 18, 19 days	Present	Present	Present
S. reflexa				
L. stagnalis				
P. gyrina	21, 28 days	Present	Present	Present
H. trivolvis				
G. hirsutus				
L. stagnalis	6 mos.	Present	Present	Present

foot musculature of five snail species (S. reflexa, L. stagnalis, P. gyrina, H. trivolvis, and G. hirsutus) were morphologically similar and apparently had attained similar levels of development. Such rediae had increased in size and each possessed the characteristic fusiform body with two posterior appendages, a tail, a pharynx, sacciform intestine, and germinal masses (Fig. 7).

The posterior appendages and the tail are locomotor in function and enable C. oculeum rediae to migrate throughout the molluscan host. The muscular pharynx surrounding the oral opening draws food material into the sacciform intestine. The nature of the intestinal contents, varying from green to brown in living specimens, is poorly understood. However, in the intestinal contents of a single redia sectioned 6 months post-exposure, epithelial cells, probably of host origin, could be seen.

Germinal masses were present in in situ sections of 7- and 8-day-old rediae located in the mantle cavity of G. hirsutus (Fig. 8).

Within C. oculeum rediae present in G. hirsutus sectioned 12 days post-exposure, beginning of cercarial development could be observed. Young cercariae were distinguished from germinal masses within the rediae by the former's elongate shape and recognizable acetabula (Fig. 9).

Fourteen days post-exposure, rediae within the following five species of snails (L. stagnalis, P. gyrina, G. hirsutus,

S. reflexa, and H. trivolvis) were producing cercariae (Fig. 10). Cercariae were found not only within rediae, but also in the foot musculature, kidney, albumin gland, mantle cavity, and connective tissue around the digestive tract (Fig. 11). These cercariae had left the rediae via a birth pore located in the anterior fifth of the rediae. Observations on living rediae indicated that cercariae were greatly constricted as they passed through the birth pore.

G. hirsutus harbored no redial stages 15 or 16 days post-exposure to miracidia. However, 17, 18, and 19 days after exposure, metacercariae were observed within the sectioned G. hirsutus for the first time. These larvae were located in the foot musculature (Fig. 12) and in connective tissue surrounding the digestive tract. Cercariae were also present in these snail specimens, some within the rediae, others in adjacent tissues (Fig. 13).

Twenty-one and 28 days after exposure to miracidia, S. reflexa, L. stagnalis, P. gyrina, G. hirsutus, and H. trivolvis all harbored at least some metacercariae in their tissues which included the foot, kidney, albumin gland, mantle cavity, tentacles, retractor muscle, and the connective tissue surrounding the digestive tract (Figs. 14 and 15). Cercariae were also present in these same tissues.

Few snails were dissected later than 28 days post-exposure except for those used in feeding experiments.

Table 4. Experimental development of C. oculeum rediae in molluscan hosts (All measurements in mm)

Host	Age (weeks)	No. meas.	Body length ave. (range)	Body width ave.(range)
G. hirsutus	1	5	0.397 (0.375-0.406)	0.142 (0.024-0.34)
	2	5	0.615 (0.506-0.717)	0.146 (0.136-0.156)
	3	4	0.728 (0.672-0.891)	0.157 (0.143-0.171)
	4	4	0.872 (0.714-0.911)	0.168 (0.150-0.182)
S. reflexa	1	5	0.734 (0.598-0.848)	0.210 (0.154-0.271)
	2	4	2.074 (1.709-2.329)	0.421 (0.322-0.501)
	3	5	1.763 (1.534-0.911)	0.399 (0.303-0.408)
P. gyrina	1	6	1.047 (0.973-1.213)	0.341 (0.325-0.346)
	2	5	1.713 (1.518-1.838)	0.291 (0.238-0.367)
	3	3	2.110 (1.934-2.306)	0.374 (0.342-0.400)
	4	4	2.234 (1.871-2.314)	0.486 (0.328-0.634)

Table 4. (Continued)

Host	Diam. pharynx ave. (range)	Germinal masses	Cercariae
G. hirsutus	0.029 (0.024-0.034)	Present	Absent
	0.031 (0.031-0.032)	Present	Present
	0.034 (0.031-0.037)	Present	Present
	0.033 (0.032-0.035)	Present	Present
S. reflexa	0.033 (0.030-0.037)	Present	Absent
	0.034 (0.031-0.037)	Present	Absent
	0.033 (0.032-0.035)	Present	Present
P. gyrina	0.032 (0.030-0.034)	Present	Absent
	0.031 (0.027-0.035)	Present	Present
	0.031 (0.029-0.033)	Present	Present
	0.034 (0.032-0.035)	Present	Present

One such exception was a large specimen of L. stagnalis dissected 6 months post-exposure. This snail harbored five rediae (averaging 5.03 mm x 1.02 mm) which were still producing cercariae (Fig. 16). Over 300 cercariae and 750 metacercariae were recovered from this snail.

Measurements of rediae taken from various snails are given in Table 4. A wide range of sizes occurred, probably due to the age of rediae, size of snails, and number of rediae per infected snail.

Cercaria

Development of emerged cercariage (Fig. 17) recovered from all five species of experimental snail hosts and the rate of development in all molluscan hosts regardless of species was similar. C. oculeum cercariae are tailless, a characteristic common to all cyclocoelids described in the literature. The mouth is ventrally located and surrounded by glandular tissues that Szidat (1932) called a penetration organ and Stunkard (1934) designated an anterior organ. A slender prepharynx passes into a pharynx. The esophagus leaving the pharynx eventually bifurcates to form intestinal ceca. These ceca course laterally for a short distance, curve posteriorly, run parallel to the sides and typically join immediately anterior to the excretory bladder. Slightly anterior to the cecal loop lies a clump of cells, the anlagen of the gonads.

Pre- and postacetabular glands stain clearly in Mallory's triple stain. Some preacetabular glands stain light blue,

other preacetabular glands as well as postacetabular ones stain dark red. In addition, ducts leading from the red-staining glands to the dark red anterior organ appear red in Mallory's triple stain. The significance of this staining reaction has not been determined.

Flame cell patterns of C. oculeum cercariae have been studied by Palm (1963) and Wootton (1964) who recorded a total of 24 flame cells in these cercariae. The precise number of flame cells could not be determined in the present study.

Emerged cercariae from three species of snails (P. gyrina, S. reflexa, and G. hirsutus) were measured. Variations in size of cercariae of this species were noted by Palm (1963) when he recovered cercariae from L. ovata 25 days post-exposure. His measurements, however, fall within the ranges presented in Table 5, indicating a wide range in variation of cercariae within the same species of snail and also from different species of snails.

Metacercaria

Cyclocoelid cercariae are known to encyst within the molluscan hosts. C. oculeum metacercariae were found in the retractor muscle, foot, tentacles, kidney, albumin gland, mantle cavity, and connective tissue surrounding the digestive tract, and may encyst within these areas as early as 17 days post-exposure (Figs. 12, 14, and 15). All five species of

Table 5. Measurements of living C. oculeum cercariae from various snail hosts (All measurements in mm)

Host	Age of rediae in days	No. rediae examined	Range of cercariae per rediae	No. meas.	Body length ave. (range)	Body width ave. (range)
P. gyrina	7	6	0			
	14	5	9-12	8	0.754 (0.579-0.903)	0.156 (0.142-0.199)
	21	3	11-13	10	0.756 (0.713-0.814)	0.266 (0.192-0.314)
	28	4	10-13	10	0.732 (0.689-0.803)	0.173 (0.124-0.291)
S. reflexa	7	5	0			
	14	4	8-14	8	0.672 (0.598-0.731)	0.156 (0.143-0.168)
	21	5	7-11	7	0.649 (0.592-0.702)	0.157 (0.146-0.165)
G. hirsutus	7	5	0			
	14	5	6-9	6	0.336 (0.303-0.354)	0.133 (0.119-0.143)
	21	4	7-10	7	0.342 (0.314-0.358)	0.128 (0.109-0.137)
	28	4	11-14	11	0.358 (0.342-0.371)	0.136 (0.126-0.152)

snail hosts harbored fully formed metacercariae. Measurements of metacercariae from four species are presented in Table 6. As this table indicates, there is very little variation in size.

Within the cyst, each metacercaria lies folded upon itself, completely filling the cyst cavity. Even though its movements are limited within the cyst, it was quite active when alive.

Encysted metacercariae are difficult to section and, when stained with Heidenhain's iron haematoxylin or Mallory's triple stain show little difference in internal structure from cercariae. Especially prominent within some of the triply stained metacercariae are red-staining glands found between the intestinal ceca.

Table 6. Measurements (in mm) of living encysted C. oculeum metacercariae from four species of snails

Snail Host	No. metacercaria measured	Diameter ave. (range)
P. gyrina	15	0.252 (0.244-0.270)
S. reflexa	20	0.249 (0.248-0.256)
G. hirsutus	20	0.254 (0.251-0.258)
H. trivolvis	20	0.253 (0.247-0.256)

Pathology

Much has been written about pathology of redial infections in molluscan hosts. Dawes (1946) stated that organs such as the digestive gland and gonads of snail hosts are greatly damaged by Fasciola hepatica larvae. He added that these organs were displaced rapidly with redial tissue. Cheng (1962) found that the digestive gland of Helisoma trivolvis was damaged to such a great extent by Echinoparyphium sp. rediae that only a few tubules remained intact. He attributed this destruction to the ingestion of cells by rediae since fragments of epithelial cells were seen within their digestive tracts.

According to Wright (1966), albumin glands of infected molluscs are replaced by tissue of parasite origin. The albumin gland is probably the first part of the snail's reproductive system to be damaged as a result of the parasite's demand for food. Because this gland supplies nutriment to the developing snail embryos, egg production and hatchability are lowered when it is damaged.

Smyth (1966) stated that the damaging effects of trematode larvae in the foot of snails range from slight to very severe. The determining factor for the degree of damage seems to be the number and size of larvae present.

To determine extent of damage to molluscan hosts of C. oculeum, sections of G. hirsutus, S. reflexa, and H. trivolvis

were examined. Rediae, cercariae, and metacercariae were found in kidney, albumin gland, foot musculature, tentacles, retractor muscle, and connective tissue surrounding the digestive tract. Usually, larvae appeared to elicit little host response. However, during the current investigation, some response to a metacercaria in an infected snail 28 days post-exposure was observed (Fig. 14). The darkly stained cells surrounding the metacercaria probably represent an attempt by the host to isolate the parasite. This was the only incident noted of any walling off. It is interesting to note that metacercariae in general apparently seldom provoke a marked response from a molluscan host (Wright, 1965).

Feeding Experiments

During this study, four laboratory-reared American Coots (Table 7) varying in age from 1 to 53 days were experimentally fed metacercariae of C. oculeum derived from S. reflexa and H. trivolvis. All hosts were exposed to metacercariae more than once. Of these hosts, two became infected. One harbored five gravid cyclocoelids; the other, one mature and five gravid cyclocoelids. Because variously aged coots were subjected to multiple exposures of metacercariae, the particular age of adult trematodes in infected birds could not be determined. Likewise, the length of time required for the fluke to mature cannot be stated precisely. However, approximations can be made.

One week after exposure of one coot to C. oculeum metacercariae from S. reflexa, its drinking water was examined daily for miracidia. Such examinations were made because, in nature, C. oculuem miracidia leave the coot via its external nares as it feeds. Miracidia were seen swimming in the water dish of this coot 6 weeks after its first dose of C. oculeum metacercariae from experimentally infected S. reflexa. Miracidia thus obtained were exposed to 10 laboratory-reared P. gyrina. Twenty-eight days later, eight of these snails harbored metacercariae of C. oculeum, thus proving the viability of the miracidia.

The longest time required for C. oculeum metacercariae to develop into gravid adults was approximately 6 weeks. Although this amount of time elapsed between the first feeding and the first observations of miracidia in the coot's drinking water, it is possible that the bird acquired its infection as a result of subsequent feedings (Table 7) and hence less than 6 weeks would be required for development. Sixteen days after miracidia appeared in the coot's drinking water, it was necropsied. At this time (58 days post-exposure), five gravid C. oculeum were recovered from the nasal cavities and orbits (Fig. 1). A thorough examination of this coot revealed no cyclocoelids in other organs.

A thorough examination of a second coot performed 40 days post-exposure indicated it to be negative for cyclocoelids.

Table 7. Feedings of C. oculeum metacercariae to laboratory-reared Fulica americana

Coot number	Molluscan intermediate host	Age of infection in snail (in days)	Number metacer-cariae fed	Age of coot (in days)	Age of infection (no. days after first feeding)	Number cyclo-coelids recovered
1	Stagnicola reflexa	53	97	3	58	5
	"	42	75	7		
	"	92	100	30		
	"	89	53	40		
2	Helisoma trivolvis	37	38	1	40	0
	"	44	57	7		
3	Helisoma trivolvis	37	83	1	53	6
	"	58	64	28		
4	Helisoma trivolvis	50	39	30	58	0
	"	72	48	53		

A third coot (53 days post-exposure) had five C. oculeum adults in its orbits and nasal cavities and one in an abdominal air sac. Specimens recovered were in varying stages of development. Four of the flukes, including the one from the air sac, contained actively moving miracidia, the fifth had the posterior third of its uterus filled with yolk and developing miracidial embryos, and the sixth was mature but non-gravid (Fig. 2). The last fluke possessed what appeared to be remnants of the anterior organ and internal glands, the latter situated in the same region as the characteristic pre- and postacetabular glands of C. oculeum cercariae. These glands exhibited staining reactions similar to those characteristic of acetabular glands of C. oculeum cercariae. Ginetzinskaja (1949) recovered young C. oculeum (=Hyptiasmus oculeus) from the head and neck muscles of naturally infected European Coots (Fulica atra) and her sections of these flukes stained with Mallory's triple stain also indicated the presence of intercecal glands extending from the gonads to the esophagus. These glands (Fig. 2) in the youngest trematode recovered from the third coot are very probably vestiges of cercarial pre- and postacetabular glands.

A fourth coot examined 58 days after being exposed to metacercariae from H. trivolvis was not parasitized.

Table 8 summarizes the results of feeding experiments with birds other than the American Coot. Four chicks (Gallus

Table 8. Feedings of C. oculeum metacercariae to birds other than Fulica americana

Snail host of C. oculeum metacercariae	Experimental bird hosts	No. metacercariae fed	Days of exposure (birds)	No. cyclocoelids recovered
Physa gyrina	Young chicken	11	58	None
Physa gyrina	Young chicken	112	58	None
Helisoma trivolvis	Gallinule	13	5	None
Lymnaea stagnalis	Young chicken	500	39	None
Lymnaea stagnalis	Young chicken	250	39	None

domesticus) and one young Common Gallinule (Gallinula chloropus) did not become infected after ingesting C. oculeum metacercariae indicating that host-specificity is apparently quite marked in this species. Wootton (1964) also fed C. oculeum metacercariae to domestic ducks and chickens but recovered no cyclocoelids. Palm (1963) apparently did not attempt any feeding experiments in his work on larval development of this trematode species.

Unfortunately, the migration pathway of C. oculeum could not be traced. Other workers who described life cycles of flukes in the family Cyclocoelidae (Szidat, 1933, Ginetzinskaja, 1954, and Ingersoll, 1954) have discussed aspects of trematode migrations within the definitive hosts. Typhlocoelum sisowi metacercariae, after being ingested by a bird, excyst in the small intestine and migrate to the bird's respiratory passages (Szidat, 1933). Szidat was unable to determine whether larval cyclocoelids migrated to the bird's lungs via the coelom or the blood vessels. However, 6 days after he fed metacercariae to domestic ducks, Szidat (1933) found young trematodes in the lungs and tracheae. The young T. sisowi were three times as long as the cercariae he found in the snail; they showed only slight structural changes. After 4 weeks in the avian host, the anterior organ was almost unrecognizable. However, the acetabulum could be seen despite the presence of many eggs in the uterus. Six weeks were required for the trematode to reach sexual maturity.

Ginetzinskaja (1949), while studying Cyclocoelum mutabile (=Cyclocoelum microstomum), fed metacercariae from laboratory-reared snails (Lymnaea ovata) to the European Coot. Eighteen hours later, young C. mutabile were in the bird's blood stream and liver. After feeding on liver parenchymal cells, young trematodes migrated to the air sacs near the heart and dorsal aorta. Ingersoll (1954) obtained the same results when he worked on the migratory pathways of this species.

STUDIES ON RELATED SPECIES

Adult Cyclocoelum brasilianum from Greater and Lesser Yellowlegs, adult Cyclocoelum obscurum from Wilson's Snipes, and adult C. vanelli from American Avocets are parasitic in the air sacs of their hosts.

Larval development is similar in the first two species. Eggs are released into water, and after hatching, the miracidia (each containing a redia) attach to aquatic snails. Redia bore into the molluscan host, leaving the empty miracidium behind. Encysted cercariae with poorly defined internal structures are seen within the rediae as early as 14 days post-exposure. From 14 days on, the number of metacercariae increases within the rediae. C. brasilianum larvae develop through the metacercarial stage in G. hirsutus of all ages as well as in recently hatched S. reflexa. Larvae of C. obscurum develop in all ages of G. hirsutus.

C. vanelli miracidia hatch in utero like those of C. oculeum. Rediae from these miracidia develop in G. hirsutus, P. gyrina, and H. trivolvis. These rediae eventually produce cercariae with poorly defined internal structures similar to cercariae of C. brasilianum and C. obscurum. However, instead of encysting within the rediae producing them, they encyst in snail tissue as do cercariae of C. oculeum.

Cyclocoelum brasilianum

Of the species of shorebirds known to migrate through Iowa, only three have been reported by Dubois (1959) to harbor C. brasilianum, namely: Greater and Lesser Yellowlegs, and Solitary Sandpipers. In the present study, 62 Lesser Yellowlegs, 22 Greater Yellowlegs, and seven Solitary Sandpipers were examined. The incidience of infection of C. brasilianum was 24%, 32%, and 0%, respectively.

Dubois (1959) listed the following as synonyms for C. brasilianum, a trematode parasite of Lesser Yellowlegs first reported and described by Stossich (1902):

Cyclocoelum (Haematotrephus) brasilianum Stossich (1902)

Synonyms:

Cyclocoelum brasilianum Stossich, 1902. p. 1-40.
Cyclocoelum halli Harrah, 1922. p. 219-328.
Cyclocoelum nitanyense Zeliff, 1946. p. 340-342.
Monostomum sp. Stossich, 1902. p. 1-40.
Cyclocoelum brasilianum Travassos, 1921. p. 121-123.

Egg

Eggs of C. brasilianum are golden brown in color, relatively thick-walled, and operculate (Fig. 18). Measurements of 10 viable eggs averaged 0.168 x 0.082 mm. These eggs are similar to eggs of C. obscurum which will be discussed later.

Miracidium

In well-developed eggs, the anterior end of the miracidium is pressed against the operculum. A few minutes after eggs were placed in previously boiled aquarium water, ciliary action of

the miracidium could be observed. Within 30 to 60 minutes, the operculum opened and the miracidium escaped. It was difficult to measure living miracidia accurately because of their constantly changing shape, but recently hatched miracidia measure approximately 0.230 x 0.090 mm (Fig. 19), and, like miracidia of C. oculeum, are positively phototactic and negatively geotactic.

Although the number of epidermal plates was not determined, four tiers are present. This number seems to be typical of cyclocoelid miracidia, for four tiers also appear in C. oculeum and in miracidia of Cyclocoelum jaenschi as reported by Johnston and Simpson (1940).

Within each C. brasilianum miracidium is a well-developed redia possessing hind appendages and a digestive tract. No definite number of flame cells in the redia within the miracidium could be determined because of the paucity of material.

Miracidia of C. brasilianum appear to be somewhat host-specific for G. hirsutus, although in two instances, development through the metacercarial stage was observed in snails of two other species (Table 9). Table 9 shows the results of exposing six species of snails representing six genera (S. reflexa, P. gyrina, H. trivolvis, L. stagnalis, G. hirsutus, and Oxyloma sp.) to miracidia of C. brasilianum taken from Greater and Lesser Yellowlegs. Two rediae of C. brasilianum were found in one of 35 experimentally exposed H. trivolvis at 28 days

Table 9. Experimental infections of snails with C. brasilianum rediae

Bird host	Snail host	No. exposed	No. infected	No. rediae recovered	Age of rediae in days (range)
G. Yellowlegs					
	P. gyrina	7	0	0	
	H. trivolvis	35	1	2	(28)
	S. reflexa	6	2	16	(30-48)
	G. hirsutus	97	38	83	(7-90)
L. Yellowlegs					
	P. gyrina	46	0	0	
	H. trivolvis	39	0	0	
	L. stagnalis	9	0	0	
	S. reflexa	5	0	0	
	G. hirsutus	38	19	41	(7-90)
	Oxyloma sp.	4	0	0	

post-exposure. Two of six recently hatched S. reflexa also became infected after being exposed to C. brasilianum miracidia for approximately 2 hours.

The single infection of H. trivolvis is somewhat surprising. Rediae of C. brasilianum may have become established in S. reflexa because the snail hosts were recently hatched. Kendall (1950) discussed age of molluscan hosts in relation to their susceptibility to Fasciola hepatica and showed that although

Lymnaea truncata appears to be the only normal intermediate host of F. hepatica in Britain, other species may become experimentally infected as well. Complete development of larval stages occurred in Lymnaea stagnalis, Lymnaea palustris, and Lymnaea globra. In Lymnaea pereger, development proceeded only to the redial stage. L. truncata was susceptible at any age or size, but the other species were susceptible only during the first few days after hatching.

When it became established that G. hirsutus served as the most suitable host for C. brasilianum, this species was used in almost all subsequent life history studies.

Experimentally, miracidia of C. brasilianum rarely attach to snails other than G. hirsutus. If they do contact other snails, they usually move about on the surface of the snail and then swim away. However, when miracidia encounter G. hirsutus, they readily attach to the foot, mantle, or tentacles of this molluscan host.

Redia

Rediae 7 days post-exposure are fusiform and possess hind appendages which are locomotor in function. The digestive system of a redia consists of an oral opening, a muscular pharynx, and a simple sacciform intestine extending approximately to the anterior edge of the hind appendages. Within rediae at this stage can be seen many germinal masses (Fig. 20). Rediae of this age are indistinguishable from those of the 7-day-old

rediae of C. oculeum (Fig. 7), and are large enough so that they may be observed through the transparent shell of G. hirsutus. Within the snail, rediae constantly migrate between the anterior portion of the foot and the albumin gland. Rarely in this study were rediae seen posterior to the ovotestis or digestive gland.

Rediae 14 days post-exposure were also clearly seen inside the living snail (Fig. 21). These rediae were not much larger than 7-day-old rediae, but within each, cercariae and metacercariae were observed. Cercariae and metacercariae are characterized by possessing an anterior organ, oral opening, acetabulum, and gonadal anlage. C. brasilianum rediae differ from those of C. oculeum in that metacercariae of the former species encyst within the rediae (Fig. 22).

A 21-day-old redia (Fig. 23) taken from G. hirsutus contained a greater number of metacercariae than did the 14-day-old redia. At least nine metacercariae and five cercariae were present in the older redia. Internal morphology of cercariae is best seen by use of sectioned rediae. A redia sectioned 21 days post-exposure showed cercariae with an anterior organ, acetabulum and darkly stained cells in the posterior third of the cercariae (Fig. 24). These cells are probably similar to cells that Stunkard (1934) found in cercariae of Typhlocoelum sisowi, and claimed by him to give rise to gonads.

Four weeks post-exposure, all redia removed from G. hirsutus contained metacercariae. A photomicrograph of one of

these rediae (Fig. 25) showed 16 metacercariae. In other respects, this redia differed little from the 21-day-old redia (Fig. 23). Sections of G. hirsutus containing rediae indicated that these larval stages were located in connective tissue around the digestive tract and in the albumin gland.

One S. reflexa, examined 30 days post-exposure, contained 14 rediae. This particular snail had been exposed to C. brasilianum immediately after the snails hatched. Numerous cercariae and metacercariae were found within these rediae.

Numerous snails died 5 weeks after exposure to miracidia of C. brasilianum. The cause of death was uncertain. However, about the same time the snails died, algae in their aquarium precipitated. This combination of unfavorable environmental conditions and parasitism may have caused their death. These snails were fixed in Bouin's fluid approximately 4 hours after death and subsequently sectioned. Rediae in sectioned G. hirsutus were found in the foot musculature, connective tissue around the digestive tract and in the albumin gland.

Forty-eight days post-exposure, one redia recovered from G. hirsutus contained 39 metacercariae. The only noticeable difference between this redia and one 28-days-old was that the older redia was larger and contained more metacercariae. Two rediae were also taken from S. reflexa 48 days post-exposure. One redia contained approximately 50 metacercariae; the other, about 15 cercariae and 20 metacercariae. Because so few cercariae and metacercariae were within the second redia,

it was assumed that cercariae had left the redia and encysted within the snail. However, a thorough search of snail tissue revealed no cercariae or metacercariae of C. brasilianum.

Fifty-six days post-exposure, a single G. hirsutus was dissected and one particularly large redia was recovered which measured 1.300 x 0.300 mm, and contained 59 metacercariae (Fig. 26).

Variations of living and fixed rediae at different ages are indicated in Tables 10 and 11. Sizes of cyclocoelid rediae are probably influenced by number of rediae per snail host, size of molluscan host, and incubation temperatures of infected snails.

Cercaria

The following structures were observed in stained, sectioned cercariae within C. brasilianum rediae: oral opening, anterior organ, acetabulum, and gonadal tissue. The well-defined digestive tract, seen in cercariae of C. oculeum, was not seen in these cercariae, nor were intercecal glands discernable.

Metacercaria

Metacercariae of C. brasilianum appear to have the same internal structures possessed by the cercariae. These are two layers in the cyst wall of C. brasilianum, in contrast to metacercariae of C. oculeum which have three (the outer layer probably of host origin).

Table 10. Measurements (in mm) of fixed *C. brasilianum* rediae recovered from *G. hirsutus*

Age (days)	Number measured	Body length ave. (range)	Body width ave. (range)
7	4	0.449 (0.360-0.546)	0.157 (0.114-0.261)
14	6	0.665 (0.029-0.687)	0.159 (0.145-0.261)
21	5	0.488 (0.410-0.550)	0.148 (0.140-0.156)
28	3	0.772 (0.759-0.796)	0.211 (0.208-0.213)
56	2	0.999 (0.918-1.080)	0.352 (0.324-0.380)

Table 11. Measurements (in mm) of living *C. brasilianum* rediae recovered from *G. hirsutus*

Age (days)	Number measured	Body length ave. (range)	Body width ave. (range)
7	4	0.687 (0.644-0.750)	0.181 (0.171-0.193)
14 14	4	0.519 (0.403-0.594)	0.188 (0.183-0.194)
21	4	0.662 (0.570-0.890)	0.191 (0.150-0.294)
28	5	0.888 (0.880-0.990)	0.240 (0.203-0.280)
48	1	1.100	0.320
56	1	1.300	0.300

Pharynx ave. (range)	Germinal masses	Cercariae	Number metacercariae
0.026 (0.026-0.027)	Present	Absent	0
0.033 (0.031-0.036)	Present	Present	0-2
0.030 (0.026-0.032)	Present	Present	1-7
0.042 (0.040-0.042)	Present	Present	7-9
0.036 (0.036)	Present	Present	42-48

Pharynx ave. (range)	Germinal masses	Number cercariae	Number metacercariae
0.032 (0.031-0.033)	Present	0	0
0.031 (0.030-0.031)	Present	6-8	0-4
0.036 (0.031-0.045)	Present	5-7	2-16
0.042 (0.042-0.043)	Present	2-6	10-16
0.035	Present	---	---
0.045	Present	3	59

Table 12. Measurements (in mm) of living C. brasilianum cercariae and metacercariae within rediae

Age of rediae in days	Number rediae examined	Range of cercariae per redia	Number measured	Body Length ave. (range)
7	4	0		
14	4	6-8	5	0.128 (0.110-0.145)
21	4	5-7	5	0.123 (0.120-0.135)
28	5	2-6	3	0.127 (0.110-0.140)
56	1	3	3	0.145 (0.130-0.160)

Body width ave. (range)	Number metacercariae per redia	Number measured	Diameter ave. (range)
	0		
0.080 (0.075-0.090)	0-4	4	0.076 (0.075-0.080)
0.085 (0.075-0.090)	2-16	5	0.085 (0.080-0.090)
0.080 (0.070-0.090)	10-16	10	0.081 (0.075-0.090)
0.085 (0.080-0.090)	59	10	0.075 (0.070-0.090)

Measurements of cercariae and metacercariae within rediae taken from G. hirsutus are given in Table 12.

Feeding experiments

Feeding experiments to Killdeers, summarized in Table 13, commenced when rediae containing metacercariae were 48 days old. Ten G. hirsutus, containing a total of 18 rediae, were fed to a laboratory-reared Killdeer. Since it is assumed that each redia contained approximately 45 metacercariae, the Killdeer probably received approximately 800 metacercariae. A wild Killdeer was fed two 48-day-old rediae taken from S. reflexa. One redia contained about 50 metacercariae and the other about 20.

Nineteen rediae 56 days post-exposure taken from 30 G. hirsutus were fed to another wild Killdeer. Fourteen days later this Killdeer received a second dose of three 70-day-old rediae.

Ninety days post-exposure, three rediae were removed from two G. hirsutus and were subsequently fed to a laboratory-reared Killdeer.

Because none of the Killdeers became infected (Table 13), that bird seems to be an unsuitable host for C. brasilianum. Greater and Lesser Yellowlegs, the normal definitive hosts

Table 13. Results of feeding experiments of C. brasilianum rediae containing metacercariae to laboratory-reared and wild Killdeers

Killdeer	Redial source	Redial age (in days)	Number rediae	Number metacercariae fed (approx.)	Necropsied (Days post-exposure)	Trematodes recovered
Laboratory reared	G. hirsutus	48	18	800	80	0
Wild	S. reflexa	48	2	70	80	0
Wild	G. hirsutus	56[1] 70[1]	19 3	850 150	70	0
Laboratory reared	G. hirsutus	90	3	150	90	0

[1]A feeding of 56-day-old rediae which contained metacercariae to this Killdeer was followed 14 days later by an exposure to 70-day-old rediae.

for C. brasilianum, breed in northern Canada and unfortunately were unavailable for the present study. Instead, Killdeer, one of the few shorebirds breeding in Iowa, was used. According to Dubois (1965), Cyclocoelum vanelli parasitizes the Killdeer.

Cyclocoelum obscurum

Dubois (1959) considered the following cyclocoelids as synonyms of Cyclocoelum obscurum Leidy, 1887:

Monostomum obscurum Leidy, 1887. p. 20-24.
Cyclocoelum sp. Looss, 1899. p. 521-784.
Cyclocoelum problematicum Stossich, 1902. p. 1-40.
Cyclocoelum exile Stossich, 1902. p. 1-40.
Cyclocoelum obliquum Harrah, 1921. p. 162-165.
Cyclocoelum leidyi Harrah, 1922. p. 219-328.
Cyclocoelum cuneatum Harrah, 1922. p. 219-328.
Cyclocoelum macrorchis Harrah, 1922. p. 219-328.
Cyclocoelum toratsugumi Morishita, 1924. p. 158-164.
Cyclocoelum orientale Witenberg, 1923. p. 1-61.
Cyclocoelum orientale var. eurhinus Tubangui, 1932. p. 369-404.
Cyclocoelum makii Yamaguti, 1933. p. 1-134.
Cyclocoelum capellum Khan, 1935. p. 342-370.
Cyclocoelum allahabadi Khan, 1935. p. 342-370.
Cyclocoelum indicum Khan, 1935. p. 342-370.
Cyclocoelum erythropis Khan, 1935. p. 342-370.
Cyclocoelum mehrii Khan, 1935. p. 342-370.
Cyclocoelum lobatum Khan, 1935. p. 342-370.
Cyclocoelum mutabile Bychowskaja-Pawlowskaja, 1953. p. 5-116.
Cyclocoelum obscurum Macko, 1964. p. 149-159.

According to Macko (1965b), morphological criteria used to identify species of the genus Cyclocoelum overlap considerably. He felt that a single criterion is insufficient for species determination and that a combination of characters must be used. Working with C. obscurum from seven different species of

shorebirds, he noted a great variation in pharynx size, shape and shape of testes and ovary, and position of the genital pore.

Harrah (1922) reported Cyclocoelum obscurum from the Willet (Catoptrophorus semipalmatus). He also reported this species of Cyclocoelum obliquum from the Wilson's Snipe (Capella gallinago) and as Cyclocoelum macrorchis from the Long-Billed Curlew (Numerius americanus). C. obscurum has also been collected in Europe, Russia, Turkey, Egypt, China, and Japan.

C. obscurum is of interest because it is most closely related to C. brasilianum (Harrah, 1922). However, Dubois (1959) placed C. obscurum in the subgenus Cyclocoelum and C. brasilianum in the subgenus Haematotrephus. The present investigation indicates that larval development of C. brasilianum and C. obscurum is similar and hence the two species should not be in two different subgenera. The validity of Dubois' subgenera will be discussed later.

Of 40 Wilson's Snipes collected in Iowa from 1966 to 1968, three (8%) were infected with C. obscurum. A second snipe was parasitized with two gravid flukes whose eggs were not developed Nevertheless, eggs from these two trematodes were fed to five laboratory-reared snails (G. hirsutus) in the hope of following further development. Seven days post-exposure, these snails were dissected and found to be negative for rediae of C. obscurum. Three gravid trematodes containing well-developed

miracidia were recovered from the abdominal air sacs of a third bird. Results of exposing S. reflexa, P. gyrina, and G. hirsutus to these miracidia are discussed below.

Egg

Eggs are operculate and possess light brown shells. Five unfixed eggs averaged 0.173 x 0.083 mm (Fig. 27) and resembled those of C. brasilianum (Fig. 18).

Miracidium

A miracidium fills its egg shell, is quite active, and its anterior end lies near the operculum. Miracidia hatched approximately 30 minutes after leaving the trematode's uterus, and, as each passed through the opercular opening of the egg, the body constricted. Living miracidia average approximately 0.260 x 0.080 mm (Fig. 28).

They swim in a random fashion until they contact snails, and appear to be negatively geotactic and positively phototactic. Many times after contact had been made they did not attach, but moved about on the surface of the molluscan host and then swam away. In other instances, miracidia attached immediately to the foot, tentacles, mantle edge, or head (Fig. 29). After attachment, the enclosed redia penetrated the snail, leaving the empty miracidium behind.

Redia

Miracidia obtained from C. obscurum were exposed to laboratory-reared snails, namely: 20 S. reflexa, 20 P. gyrina, and 10 G. hirsutus. Miracidia attached to all three of the above species. However, 8 days post-exposure, no trematode larvae were found in S. reflexa and P. gyrina. However, G. hirsutus were infected with rediae of C. obscurum.

Eight days post-exposure, one G. hirsutus was examined. Five rediae were recovered (Fig. 30), all quite similar to 7-day-old rediae of C. brasilianum and C. oculeum (Figs. 20 and 7). They all possessed a tail, posterior appendages, a pharynx, a sacciform intestine, and germinal masses.

Fourteen days post-exposure, two G. hirsutus were dissected. One snail harbored four rediae; the other contained one. All rediae appeared similar to 8-day larvae except for their larger size and the presence of cercariae (Fig. 31). One of the rediae also contained metacercariae. In sectioned material, cercariae appear similar to those of C. brasilianum, for each possesses an anterior organ, oral opening, and acetabulum. In addition, there is a cluster of deeply staining cells near the posterior end. These cells are probably similar to cells Stunkard (1934) found in cercariae of Typhlocoelum sisowi, which he considered to be fundaments of gonads.

Twenty-one days post-exposure, one G. hirsutus harbored four rediae (Fig. 32), one of which contained seven cercariae

and 16 metacercariae. Rediae sectioned at this stage showed the same internal structures as did 14-day-old rediae except for an additional number of metacercariae.

Twenty-eight days post-exposure, four rediae were recovered from specimens of G. hirsutus (Fig. 33). These rediae differed little from 21-day-old rediae.

As rediae developed, they usually became larger and contained more metacercariae (Table 14). Sizes of cercariae and metacercariae within rediae are shown in Table 15. Although cercariae and metacercariae of C. obscurum are somewhat larger than those of C. brasilianum, the difference is probably not significant. C. obscurum rediae appear to develop in the same manner as those of C. brasilianum. Because of the paucity of additional infected G. hirsutus, no more infected snails were opened, but were saved for later feeding experiments.

The remaining snails were kept under close observation in the laboratory. Their small size and transparent shell greatly facilitated observations of redial migration. Rediae within G. hirsutus move actively from the region of the head-foot to the albumin gland. However, they are most frequently found in the mantle chamber. With proper lighting, metacercariae within rediae may be seen under the dissecting microscope.

Ninety days post-exposure, two of the 10 G. hirsutus previously exposed to miracidia of C. obscurum remained. These two snails were infected, one with a single redia, the other

Table 14. Development of Cyclocoelum obscurum rediae. (Data from fixed and living specimens; all measurements in mm).

Type	Age (days)	Number measured	Body length ave. (range)	Body width ave. (range)
Fixed	8	2	0.555 (0.540-0.570)	0.125 (0.120-0.130)
	14	2	0.540 (0.520-0.560)	0.135 (0.120-0.150)
	21	2	0.770 (0.740-0.800)	0.175 (0.170-0.180)
	28	2	0.835 (0.730-0.940)	0.215 (0.210-0.220)
Living	8	1	0.610	0.140
	14	1	0.650	0.180
	21	1	1.010	0.240
	28	1	0.800	0.260

Table 15. Measurements (in mm) of living C. obscurum cercariae and metacercariae within rediae

Age of rediae in days	Number rediae examined	Cercariae per redia	Number measured	Body length ave. (range)
8	1	0		
14	1	5	5	0.149 (0.133-0.156)
21	1	4	4	0.185 (0.172-0.192)
28	1	3	3	0.183 (0.179-0.189)

Pharynx diameter ave. (range)	Germinal masses	Cercariae	Number metacercariae
0.025 (0.024-0.025)	Present	Absent	0
0.028 (0.027-0.029)	Present	Present	0-1
0.034 (0.034-0.034)	Present	Present	5-9
0.038 (0.037-0.038)	Present	Present	9-10
0.036	Present	Absent	0
0.036	Present	Present (7)	2
0.040	Present	Present (4)	9
0.042	Present	Present (3)	10

Body width ave. (range)	Number metacercariae per redia	Number measured	Average diameter (range)
0.074 (0.070-0.086)	2	2	0.097 (0.093-0.099)
0.067 (0.058-0.075)	9	9	0.095 (0.089-0.098)
0.070 (0.065-0.073)	10	10	0.083 (0.073-0.091)

with two. A laboratory-reared Killdeer was exposed at this time to these rediae. An accurate count of metacercariae within the rediae was not made for fear of damaging rediae or metacercariae before they were fed to the Killdeer.

Ninety days elapsed after feeding the Killdeer before it was necropsied. Its lungs, air sacs, trachea, orbits, liver, intestine, and bursa of Fabricius were examined, but no part contained cyclocoelids.

Cyclocoelum vanelli

Dubois (1965) considered the following cyclocoelids as synonyms of Cyclocoelum vanelli (Rudolphi, 1819).

Cyclocoelum (Haematotrephus) vanelli

Synonyms:

Monostoma vanelli Rudolphi, 1819. p. x-811.
Monostoma lanceolatum Wedl, 1957. p. 241-278.
Haematotrephus similis Stossich, 1902. p. 1-40.
Haematotrephus consimilis Nicoll, 1914. p. 105-126.
Haematotrephus adelphus Johnston, 1916. p. 187-261.
Uvitellina pseudocotyles Witenberg, 1926. p. 103-186.
Uvitellina magniembria Witenberg, 1926. p. 103-186.
Cyclocoelum (Uvitellina) dollfusi Tseng, 1930. p. 254-258.
Uvitellina keri Yamaguti, 1933. p. 1-134.
Uvitellina tageri Yamaguti, 1933. p. 1-134.
Uvitellina macroisophaga Hannun and Wilson, 1934. p. 245-250.
Cyclocoelum obscurum Houdemer, 1938 nec Leidy, 1887. p. 1-235.
Haematotrephus (Uvitellina) vanelli (Rudolphi) Dollfus, 1948. p. 129-199.
Uvitellina adelpha (Johnston) Bychowskaja-Pawlowskaja, 1953. p. 5-116.
Cyclocoelum titiri P. N. Chatterji, 1958. p. 559-565.
Haematotrephus (H.) lobivanelli N. K. Gupta, 1958. p. 107-111.
Haematotrephus (Uvitellina) kaniharensis P. D. Gupta, 1958. p. 1-5.

Uvitellina vanelli (Rudolphi) Macko, 1959. p. 523-530.
Uvitellina indica Siddiqi and Jairajpuri, 1962. p. 212-214.
Cyclocoelum (Haematotrephus) lanceolatum (Wedl) Stunkard, 1966. p. 209-213.
Cyclocoelum (Haematotrephus) vanelli (Rudolphi) Stunkard, 1966. p. 209-213.
Cyclocoelum lanceolatum Eckman, 1968. p. 1143.

C. vanelli is widely distributed, having been reported from various charadriiform birds in Europe, Asia, Africa, Russia, Australia, and the United States. The three United States reports of C. vanelli are those by Hannun and Wilson (1934), (reported as Uvitellina macroisophaga) from the body cavity of the Killdeer (Charadrius vociferus); Stunkard (1966), (reported as Cyclocoelum lanceolatum) from the abdominal air sacs of the American Avocet (Recurvirostra americana); and Eckman (1968) reported it as Cyclocoelum lanceolatum from the body cavity of the Killdeer.

In the present study, five American Avocets were collected 10 miles north of Sand Lake Wildlife Refuge, South Dakota. Two of the five were infected, one a male with 13 gravid trematodes in the abdominal air sacs, the other a female harboring four gravid trematodes. These cyclocoelids are apparently conspecific with those classified by Dubois (1965) as C. vanelli.

Stunkard (1966) described C. vanelli from the American Avocet. In discussing the morphology of this cyclocoelid, he stated, "The testes are spherical to oval unless deformed as a result of pressure during fixation, ...". However, in the present study, testes were either unlobed or lobed in specimens fixed without coverslip pressure (Figs. 34 and 35) and in

living trematodes. Stunkard also stated that testes measurements vary from 0.50 to 0.090 mm in diameter. Stunkard's "maximum" limit, 0.090 mm, may be an error in his paper. Macko (1960) recovered C. vanelli (=Haematotrephus lanceolatum) from the Ruff (Philomachus pugnax). Specimens obtained by him possessed both lobed and unlobed testes ranging considerably in size: 0.354-1.932 x 0.231-1.403 mm for the posterior testis, and 0.712-1.512 x 0.864-1.642 mm for the anterior testis. Testes measurements of 10 specimens of C. vanelli in the present investigation ranged in diameter from 0.756-1.598 x 0.864-1.555 mm for the posterior testis, and 0.712-1.512 x 0.864-1.642 mm for the anterior testis.

Egg

Eggs are operculate with relatively thin, fragile shells compared to the relatively thick-shelled eggs of C. brasilianum and C. obscurum. Measurements of 29 fixed intra-uterine eggs in stained whole mounts averaged 0.135 x 0.054 mm. These eggs appear to be similar to those of Cyclocoelum oculeum.

Miracidium

As noted previously, cyclocoelid eggs either hatch in utero or in water. C. oculeum, in orbits and nasal cavities of American Coots, produce eggs hatching in utero, whereas C. brasilianum and C. obscurum (in the abdominal air sacs of Greater Yellowlegs and Lesser Yellowlegs, and Wilson's

Snipe respectively) release eggs that hatch in water.

Immediately after removal of gravid C. vanelli from abdominal air sacs of American Avocets, free-swimming miracidia were noted within the uteri. If eggs of C. vanelli hatch in utero under normal conditions, miracidia thus released would have to make their way via the bronchioles and trachea to the outside.

Behavior of C. vanelli miracidia is similar to that of other cyclocoelid miracidia mentioned in the present study in that they are negatively geotactic and positively phototactic. Measurements of five miracidia in the living state averaged 0.195 x 0.061 mm.

Miracidia, when released in water, must attach to an appropriate snail host or die within approximately 2 hours. I have shown experimentally that larval development of C. vanelli may occur in G. hirsutus, H. trivolvis, or P. gyrina. It is noteworthy that redial stages of C. vanelli developed in a wider range of experimental intermediate hosts than did redial stages of C. brasilianum and C. obscurum. Figures 36, 37, 38, and 39 show the attachment of miracidia to H. trivolvis and subsequent escape of rediae into snail tissue.

Redia

One P. gyrina and one G. hirsutus were examined 7 days after having been exposed to miracidia of C. vanelli. Although P. gyrina was free of redial stages of C. vanelli, one redia

was recovered from the connective tissue around the digestive tract of G. hirsutus. It measured 0.430 x 0.090 mm and was characterized by small anterior appendages, large posterior appendages, and a tail (Fig. 40).

The small anterior appendages on this 7-day-old redia (Fig. 40) appear similar to those observed by Stunkard (1934) on Typhlocoelum sisowi rediae which he had removed from miracidia. He did not find anterior appendages on older rediae; that is, rediae recovered from snails.

One possible reason for the retention of anterior redial appendages is that redial development may have been retarded by the low temperature at which the snails were incubated. Internally, a muscular pharynx measuring 0.030 mm in diameter and a sacciform intestine extending to the posterior edge of the hind appendages could be clearly seen. No germinal masses were discernible within the redia at this time.

Fourteen days post-exposure, a single specimen of G. hirsutus and a single specimen of H. trivolvis each harbored one redia. Both rediae were recovered from the foot muscles of their respective hosts.

The redia from G. hirsutus was damaged during removal; however, the redia from H. trivolvis was removed intact. The latter redia possessed a tail, posterior appendages, pharynx, sacciform intestine, birth pore, germinal masses, and cercariae (Fig. 41). The redia measured 1.320 x 0.335 mm and its pharynx

was 0.060 mm in diameter. Three cercariae measured within the redia averaged 0.251 x 0.120 mm. A birth pore seen near the anterior one-fifth of the redia (Fig. 41) would allow for escape of cercariae. However, cercariae were not observed outside the redia at this time.

Twenty-one days post-exposure, two P. gyrina were dissected; one of them harbored a single redia (Fig. 42). Dimensions of this specimen were 0.810 x 0.330 mm for the body and 0.045 x 0.035 mm for the pharynx. Five cercariae measured within the redia averaged 0.227 x 0.075 mm. After being observed and measured, this 21-day-old redia was sectioned and stained with Heidenhain's iron haematoxylin. Sections of this redia indicated that cercariae within the redia are similar to cercariae of C. brasilianum and C. obscurum of the same age.

Twenty-eight days post-exposure, one G. hirsutus, four H. trivolvis, and one P. gyrina were examined. Only the latter was infected with one redia. This particular redia contained numerous germinal masses and cercariae. Examination of snail tissue revealed seven metacercariae averaging 0.126 mm in diameter. Internally, these metacercariae of C. vanelli resembled those of C. brasilianum and C. obscurum. Externally, C. vanelli metacercariae have a three-layered cyst wall as do metacercariae of C. oculeum.

Research was terminated at this time due to lack of infected snails.

Larval development of C. vanelli resembles that of C. oculeum, C. brasilianum, and C. obscurum in several respects. Larval development of C. vanelli appears similar to that of C. oculeum in that miracidia are found free in the uterus of the adult trematode and that metacercariae in the snail's tissues possess a cyst wall of three layers. C. vanelli rediae, like those of C. oculeum rediae, appear to develop in a wider range of snail hosts than do rediae of C. brasilianum and C. obscurum. Cercariae of C. vanelli resemble those of C. brasilianum and C. obscurum in lacking well-developed internal structures.

Cyclocoelum tringae

Dubois (1959) considered the following cyclocoelids to be synonyms of Cyclocoelum tringae Stossich, 1902.

> Monostomum tringae Brandes, 1892. (nom. nud.). p. 504-511.
> Cyclocoelum taxorchis Johnston, 1916. p. 187-261.
> Cyclocoelum tringae Stossich, 1902. p. 1-40.
> Cyclocoelum wilsoni Harrah, 1922. p. 219-328.
> Cyclocoelum triangularum Harrah, 1922. p. 219-328.
> Corpopyrum capellae Yamaguti, 1933. p. 1-134.
> Cyclocoelum tringae Bychowskaja-Pawlowskaja, 1953. p. 5-116.

This particular species is widely distributed, having been reported from Egypt, Russia, Australia, Formosa, and the United States.

Nine mature Cyclocoelum tringae were collected from the abdominal air sacs of a Pectoral Sandpiper (Erolia melanotos) in the spring of 1967. During the spring of 1968, four gravid specimens were collected from the abdominal air sacs of a second

Pectoral Sandpiper. These trematodes were used in the experiments discussed below.

Approximately 10 minutes after placing gravid C. tringae in water, eggs were released. Measurements of five living eggs averaged 0.174 x 0.082 mm. Eggs of C. tringae resemble those of C. brasilianum and C. obscurum in size, shape, and color.

Miracidial activity was evident within each egg after eggs had been released into water. Within 15 minutes after being released by the fluke, eggs began to hatch. Five living miracidia, averaging 0.244 x 0.073 mm, were similar to miracidia of C. oculeum, C. brasilianum, C. obscurum, and C. vanelli in distribution and length of cilia. Internally, a redia and a bilobed eyespot were present. They were positively phototactic and negatively geotactic.

Miracidia of C. tringae were exposed to various laboratory-reared snails, namely: 20 G. hirsutus, 5 S. reflexa, 3 H. trivolvis, and 10 P. gyrina. While being exposed, these snails were kept under constant observation. In no instance were miracidia seen to attach to these snails. To make certain redial penetration had not been overlooked, all snails were dissected 7 days later, but no rediae were recovered.

DISCUSSION

A compilation of the data on the known life cycles of cyclocoelids (Table 16) indicates a considerable lack of uniformity in the biology of this group of trematodes. Adults are found in the abdominal air sacs, tracheae, nasal cavities and orbits of at least six orders of avian hosts. Additional orders are parasitized by cyclocoelids whose life cycles are unknown. Cyclocoelid eggs may hatch in utero, in water, or within the snail host. Except for C. oculeum and C. vanelli which possess thin-walled eggs, all other species in which the life cycles are known possess relatively thick-shelled eggs. All species with thick-walled eggs hatch in water with the exception of C. elongatum whose miracidia emerge only after molluscan intermediate hosts have ingested eggs (Timon-David, 1955).

Aquatic snails serve as intermediate hosts for all cyclocoelids previously reported with the exception of C. elongatum which uses Helicopis arenosa, a terrestial snail (Timon-David, 1955).

Larval trematodes, in general, are very host-specific for their intermediate hosts. However, Table 16 indicates lack of specificity of cyclocoelids for intermediate hosts. Experimentally, C. vanelli, C. mutabile, and C. oculeum are known to develop readily in three, six, and six genera of snails, respectively. C. brasilianum, as shown in the present

Table 16. Summary of known life cycle stages of Cyclocoelids

Species	*T. sisowi*	*C. jaenschi*	*C. mutabile*	*C. elongatum*
Subgenus	---	*Haematotrephus*	*Cyclocoelum*	*Hyptiasmus*
Bird order	Anseriformes, Gruiformes	Gruiformes	Charadiiformes, Gruiformes, Galliformes	Passeriformes, Galliformes, Piciformes
Parasite location	Trachea, nasal passages	Abdominal air sacs	Abdominal air sacs	Abdominal air sacs
Egg shell	Thick-walled	Thick-walled	Thick-walled	Thick-walled
Hatching site	Water	Water	Water	Snail
Snail	*L. ovata*, *H. trivolvis*	*Ameria* sp.	*L. ovata*, *L. stagnalis*, *H. trivolvis*, *P. gyrina*, *Menetus exacuous*, *Gyraulus* sp.	*Helicopis arenosa*
Cercariae				
Oral opening	++[a]	++	+[b]	+
Anterior organ	++	++	+	+
Acetabulum	++	+?	+	+
Acetabular glands	++	+?	?	?
Gonadal anlagen	++	+?	+	+
Intestine	++	+	+	+
Metacercariae				
Layers in cyst wall	2?	?	3	2?
Location	Snail tissue	Snail tissue	Rediae	Rediae
References	Szidat (1932, 1933), Stunkard (1934)	Johnston and Simpson (1940)	Ginetzinskaja (1949, 1952, 1954), Ingersoll (1954)	Timon-David (1955)

[a] ++Well-developed.

[b] +Poorly developed.

C. oculeum	*C. brasilianum*	*C. obscurum*	*C. vanelli*
Hyptiasmus	*Haematotrephus*	*Cyclocoelum*	*Haematotrephus*
Gruiformes	Charadiiformes	Gruiformes, Passeriformes, Charadiiformes	Charadiiformes
Nasal cavity, eye orbits	Abdominal air sacs	Abdominal air sacs	Abdominal air sacs
Thin-walled	Thick-walled	Thick-walled	Thin-walled
In utero	Water	Water	In utero
L. ovata, *S. reflexa*, *G. hirsutus*, *P. gyrina*, *H. trivolvis*, *L. stagnalis*	*H. trivolvis*, *S. reflexa*, *G. hirsutus*	*G. hirsutus*	*G. hirsutus*, *P. gyrina*, *H. trivolvis*
++	+	+	+
++	+	+	+
++	+	+	+
++	0	0	0
++	++	++	++
++	?	?	?
3+	2	2	3
Snail tissue	Rediae	Rediae	Snail tissue
Palm (1963), Wootton (1964), Present study	Present study	Present study	Present study

study, readily develop in G. hirsutus, but may also develop in recently hatched S. reflexa and, in one instance, H. trivolvis.

The site of cercarial encystment (in tissues or in rediae) appears to be associated with the general level of development of certain cercarial structures. Thus, cercariae encysting in their rediae lack a well-developed oral opening, anterior organ, acetabulum, and intestine but possess a well-developed gonadal anlagen. However, cercariae encysting within the snail's tissues generally have a distinct oral opening, anterior organ, pharynx, acetabulum, acetabular glands, and intestine. The one exception to this generalization is C. vanelli in which cercariae encyst in snail tissue, but possess poorly defined internal structures.

Metacercariae within the molluscan host may localize in one of two sites depending upon the species of cyclocoelid. Some cercariae encyst within the same rediae producing them (C. elongatum, C. brasilianum, and C. obscurum) or cercariae may leave the rediae and encyst within the snail's tissues (T. sisowi, C. jaenschi, C. mutabile, C. oculeum, and C. vanelli).

All metacercariae encysting within snail tissue except for T. sisowi (as indicated in an illustration by Stunkard, 1934) have triple-layered cyst walls, whereas metacercariae encysting within rediae have double-layered cyst walls.

As indicated in an earlier section of this thesis, Dubois (1959) divided the genus Cyclocoelum into three subgenera

(Hyptiasmus, Haematotrephus, and Cyclocoelum) on the basis of certain morphological criteria of adult worms, such as position of ovary and testes, and extent and position of uterine coils. Comparative morphological studies (Macko, 1959, 1960, 1964, 1965a, 1965b; Macko and Bursa, 1960; and Macko and Feige, 1960) on adult cyclocoelids, however, have indicated marked variations within species relative to these characteristics as well as those relating to body size, extent of vitellaria, diameter of pharynx, and position of genital pore. According to Macko (1965b), morphological characters are so variable within the genus Cyclocoelum that numerous criteria must be used to define a particular species. This lack of well-defined morphological criteria between species and the considerable range of size and position of structures within a species suggest that host-induced variations may be significant.

The best experimental evidence for the fact that a particular host may influence morphological characteristics is that of Watertor (1967), who dealt with host-induced variations in adult Telorchis bonnerinsis, a trematode found in the intestine of amphibians. Through carefully controlled studies, she found that this species, when reared in turtles, closely resembled T. corti known to occur in chelonian hosts. Experimental rearing of successive generations in amphibian and reptilian hosts showed conclusively that morphological modifications may be dependent upon the host in which the parasite develops.

Her study showed that changes in the size of the parasite, extent of its vitellaria, position of ovary, extent of cirrus sac, and comparative size of suckers are all criteria subject to great variation. From this, she concluded that such criteria were unsuitable for delimiting species. Very probably similar variations within cyclocoelids are also host-induced.

On the basis of known life cycle studies, it appears that Dubois' (1959, 1965) classification is subject to question particularly at the subgeneric level. Reference to Table 16 indicates that within the subgenus Haematotrephus, one finds species whose metacercariae develop within the rediae (C. brasilianum) and species whose metacercariae encyst in molluscan tissues (C. jaenschi, C. vanelli). Species within the subgenus also vary with reference to hatching of the eggs and thickness of the egg shell. On the basis of present knowledge, it does not appear feasible to retain Dubois' subgenera. Nonetheless, his classification in other respects is of value and probably should be retained, for more than anyone else, he has brought a degree of order to a previously unmanageable group of trematodes. Additional carefully controlled experimental life cycles are needed, and until more data are forthcoming, no extensive revisions of Dubois' classification appears justifiable.

SUMMARY AND CONCLUSIONS

1. During the course of this study, 386 birds of 17 species known to serve as definitive hosts for trematodes belonging to the family Cyclocoediae were examined. Of 161 coots, 28 (17%) harbored only C. oculeum, 32 (20%) were parasitized by C. mutabile, and 17 (11%) contained both. If single and double infections are totaled, C. oculeum occurred in 45 (28%), and C. mutabile in 49 (31%) of 161 American Coots. Twenty-three Blue-Winged Teal were examined and one was parasitized with Typhlocoelum cucumerinum, a new host record. Infections of shorebirds were as follows: 2 of 5 (40%) American Avocets harbored C. vanelli, 7 of 22 (32%) Greater Yellowlegs and 15 of 62 (24%) Lesser Yellowlegs were parasitized with C. brasilianum, 2 of 14 (14%) Pectoral Sandpipers were infected with C. tringae, and 3 of 40 (8%) Wilson's Snipes contained C. obscurum. All other bird species examined were negative for cyclocoelids.

2. The life history and host-parasite relationships of the trematode C. oculeum have been experimentally determined. Adults parasitize the eye orbits and nasal cavities of the American Coot.

3. Thin-walled operculate eggs hatch in the uterus of the adult worm and release miracidia which leave the coot via its external nares when the definitive host feeds.

4. Miracidia closely resemble those of other cyclocoelids and possess 21 ciliated epidermal plates in four tiers arranged in a 6:9:4:2 pattern. Miracidia attach to and develop within S. reflexa, L. stagnalis, G. hirsutus, P. gyrina, and H. trivolvis. After attachment, the redia within the miracidium enters the snail, leaving the empty miracidium behind.

5. The highly motile redia may be found in the foot musculature, albumin gland, kidney, mantle cavity, tentacles, and connective tissue surrounding the digestive tract. Rediae are characterized by their fusiform shape and the presence of two posterior appendages.

6. Within 4 to 6 days post-exposure, germinal masses can be seen developing within the redia. At 12 to 14 days, well-developed cercariae are being produced. By 14 days, cercariae were observed in various snail tissues, foot musculature, tentacles, kidney, albumin gland, mantle cavity, and connective tissue around the digestive tract.

7. Cercariae of C. oculeum are tailless, possess an oral opening surrounded by glandular tissue, a prepharynx, pharynx, and esophagus bifurcating to form intestinal ceca and joining posteriorly in the typical cyclocoelid pattern. Anlagen of gonads, unicellular acetabular glands, and an acetabulum are also present.

8. C. oculeum rediae taken from L. stagnalis were still producing cercariae 6 months post-exposure.

9. In cercariae stained in Mallory's triple stain, red-staining pre- and postacetabular glands, and a second set of preacetabular glands staining light blue may be seen.

10. As early as 17 days post-exposure, cercariae within G. hirsutus encyst within the tissues. By 21 days, rediae in G. hirsutus, P. gyrina, H. trivolvis, S. reflexa, and L. stagnalis produce metacercariae. Internally, metacercariae appear similar to cercariae. Externally, they are surrounded by a triple-layered cyst wall. They have been recovered from the albumin gland, foot musculature, kidney, tentacles, retractor muscle, mantle cavity, and connective tissue around the digestive tract.

11. Laboratory-reared coots (the normal definitive host), if fed metacercariae from H. trivolvis or S. reflexa, become infected with adult worms. Young trematodes, upon reaching the nasal cavities and orbits, are non-gravid and possess acetabular glands and a remnant of the anterior organ. A maximum of 6 weeks is involved from ingestion of metacercariae to the presence of gravid trematodes.

12. Larval development through the metacercarial stage has been experimentally determined for C. brasilianum recovered from the abdominal air sacs of Greater and Lesser Yellowlegs. Operculate eggs hatch in water, releasing miracidia closely resembling those of other cyclocoelids and possessing four

tiers of epidermal plates.

13. Redial development through the metacercarial stage occurs in G. hirsutus of varying ages and in recently hatched S. reflexa. In one instance, two rediae containing metacercariae were recovered from H. trivolvis.

14. By 7 days post-exposure, germinal masses can be observed within rediae, and at 14 days, cercariae and metacercariae are discernible. Rediae from G. hirsutus at 21, 28, 35, 48, 56, 70, and 90 days post-exposure and from S. reflexa 30 and 48 days post-exposure increase in size and in number of contained metacercariae as their age increases.

15. Cercariae of C. brasilianum are characterized by poorly developed oral opening, anterior organ, acetabulum, and by well-developed anlagen of gonads. Metacercariae within rediae are surrounded by a double-layered cyst wall and possess the same internal structures as do cercariae.

16. Metacercariae of C. brasilianum of various ages taken from G. hirsutus or S. reflexa and fed to laboratory-reared and wild Killdeers failed to produce an infection.

17. Larval development of C. obscurum (whose adults parasitize the abdominal air sacs of Wilson's Snipe) occurs in G. hirsutus and is similar to that of C. brasilianum.

18. Larval development of C. vanelli, from the abdominal air sacs of the American Avocet, has features in common with larval development of C. oculeum, C. brasilianum, and C.

obscurum. Eggs are thin-walled and similar to those of C. oculeum. Miracidia hatch in utero, are probably released into the abdominal air sacs, and migrate through the bronchioles and trachea to the outside.

19. Redial development of C. vanelli occurs in P. gyrina, H. trivolvis, and G. hirsutus. Cercariae are similar to those of C. brasilianum and C. obscurum. However, cercariae of C. vanelli, like C. oculeum cercariae, encyst in snail tissue and possess a triple-layered cyst wall.

20. C. tringae, from the air sacs of the Pectoral Sandpiper, has eggs and miracidia resembling those of C. brasilianum and C. obscurum. G. hirsutus, S. reflexa, P. gyrina, and H. trivolvis exposed to miracidia of C. tringae were refractive to infection.

21. On the basis of known life cycle studies, it does not appear feasible to retain Dubois' (1959) subgeneric classification. However, until more data are forthcoming, no extensive revisions of Dubois' classification appears justifiable.

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PLATES

Abbreviations in Plates

a = acetabulum

ag = acetabular glands

ap = anterior appendages

bp = birth pore

c = cercaria

d = digestive tract

es = eyespot

ga = gonadal anlage

gm = germinal masses

m = metacercaria

mir = miracidium

o = operculum

p = pharynx

pa = posterior appendage

po = penetration organ

r = redia

t = terebratorium

te = testis

Plate 1

Fig. 1. Gravid *Cyclocoelum oculeum*.

Fig. 2. Mature *C. oculeum*.

Fig. 3. Epidermal plates of *C. oculeum* miracidium.

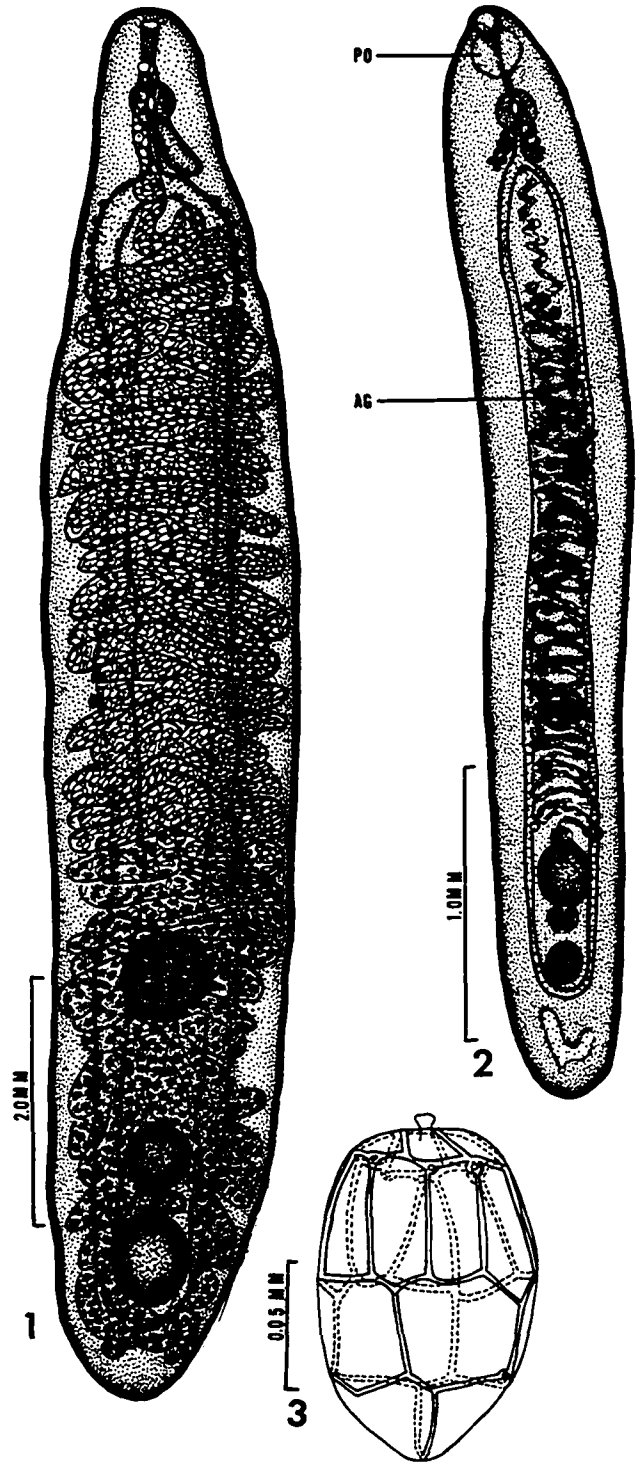
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Plate II

Figs. 4 - 10. Larval development of *C. oculeum*.

Fig. 4. Egg. Note operculum.

Fig. 5. Emerged miracidium.

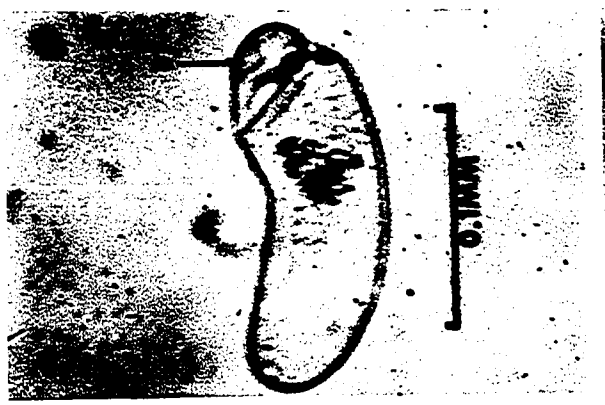
Fig. 6. Four-day-old redia *in situ* in the foot muscle of a *Gyraulus hirsutus*. Note digestive tract. (Same scale as in Fig. 4).

Fig. 7. Living redia 7 days post-exposure, from the mantle chamber of *P. gyrina*.

Fig. 8. Eight-day-old rediae in the pulmonary cavity of *G. hirsutus*. In one of the rediae, at least four germinal masses are present.

Fig. 9. Numerous 12-day-old rediae in connective tissue surrounding the digestive tract of *G. hirsutus*. Note the developing cercaria. (Same scale as in Fig. 8).

Fig. 10. Living 14-day-old redia from *Stagnicola reflexa*. Each cercaria within the redia possesses an acetabulum. (Same scale as in Fig. 7).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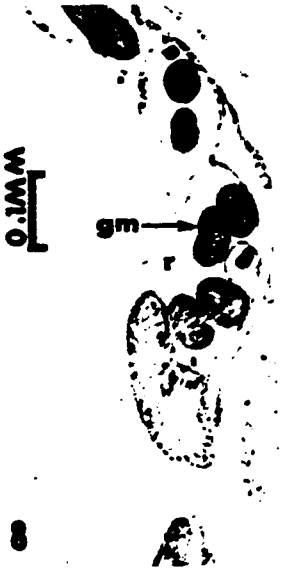
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Plate III

Figs. 11 - 17. Larval development of *C. oculeum* (continued).

Fig. 11. Cercariae in connective tissue surrounding the digestive tract of *G. hirsutus*.

Fig. 12. Metacercaria in foot muscle of *G. hirsutus* 17 days post-exposure. (Same scale as in Fig. 11).

Fig. 13. Cercaria in the foot musculature of *G. hirsutus* 17 days post-exposure. (Same scale as in Fig. 11).

Fig. 14. Metacercaria in foot muscle of *Helisoma trivolvis* 28 days post-exposure. (Same scale as in Fig. 11).

Fig. 15. Metacercaria 28 days post-exposure in tentacle of *S. reflexa*. (Same scale as in Fig. 11).

Fig. 16. Redia from *Lymnaea stagnalis* 6 months post-exposure. (Same scale as in Fig. 11).

Fig. 17. Living cercaria 14 days post-exposure.

Plate IV

Fig. 18. *C. brasilianum* egg.

Fig. 19. *C. brasilianum* miracidium. Note the two posterior redial appendages.

Fig. 20. Seven-day-old *C. brasilianum* redia from *G. hirsutus*.

Fig. 21. Rediae of *C. brasilianum* in connective tissue surrounding digestive tract of *G. hirsutus* (14 day infection).

Fig. 22. Fourteen-day-old *C. brasilianum* redia from *G. hirsutus*. (Same scale as in Fig. 20).

Fig. 23. *C. brasilianum* redia recovered 21 days post-exposure from *G. hirsutus*. Within the redia are seen approximately five cercaria and nine metacercariae. (Same scale as in Fig. 20).

Fig. 24. Sectioned *C. brasilianum* redia from *G. hirsutus* 21 days post-exposure. Note gonadal anlage. (Same scale as in Fig. 18).

Fig. 25. *C. brasilianum* redia from *G. hirsutus* 28 days post-exposure. Sixteen metacercariae are present. (Same scale as in Fig. 20).


18
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23
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Plate V

Fig. 26. *C. brasilianum* redia from *G. hirsutus* 56 days post-exposure.

Fig. 27. *Cyclocoelum obscurum* egg.

Fig. 28. *C. obscurum* miracidium. Note posterior appendages of contained redia.

Fig. 29. *C. obscurum* miracidium attached to the head of *G. hirsutus*.

Fig. 30. *C. obscurum* redia from *G. hirsutus* 8 days post-exposure.

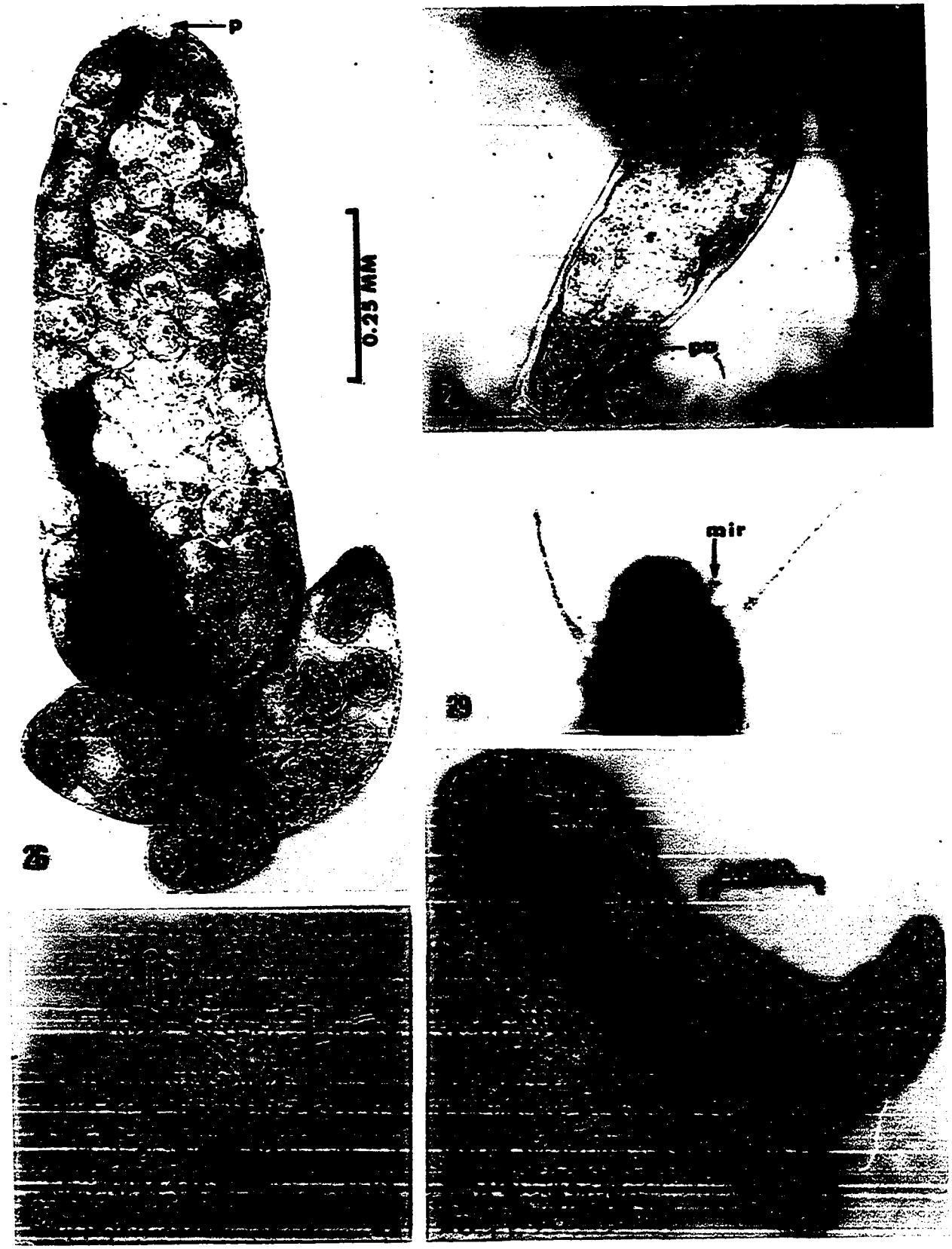
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Plate VI

Fig. 31. Fourteen-day-old C. obscurum redia from G. hirsutus.

Fig. 32. C. obscurum redia from G. hirsutus 21 days post-exposure. Note the numerous metacercariae. (Same scale as in Fig. 31).

Fig. 33. C. obscurum redia from G. hirsutus 28 days post-exposure. Note cercariae and metacercariae. (Same scale as in Fig. 31).

Figs. 34 and 35. Unlobed and lobed testes in unflattened specimens of Cyclocoelum vanelli from the American Avocet.

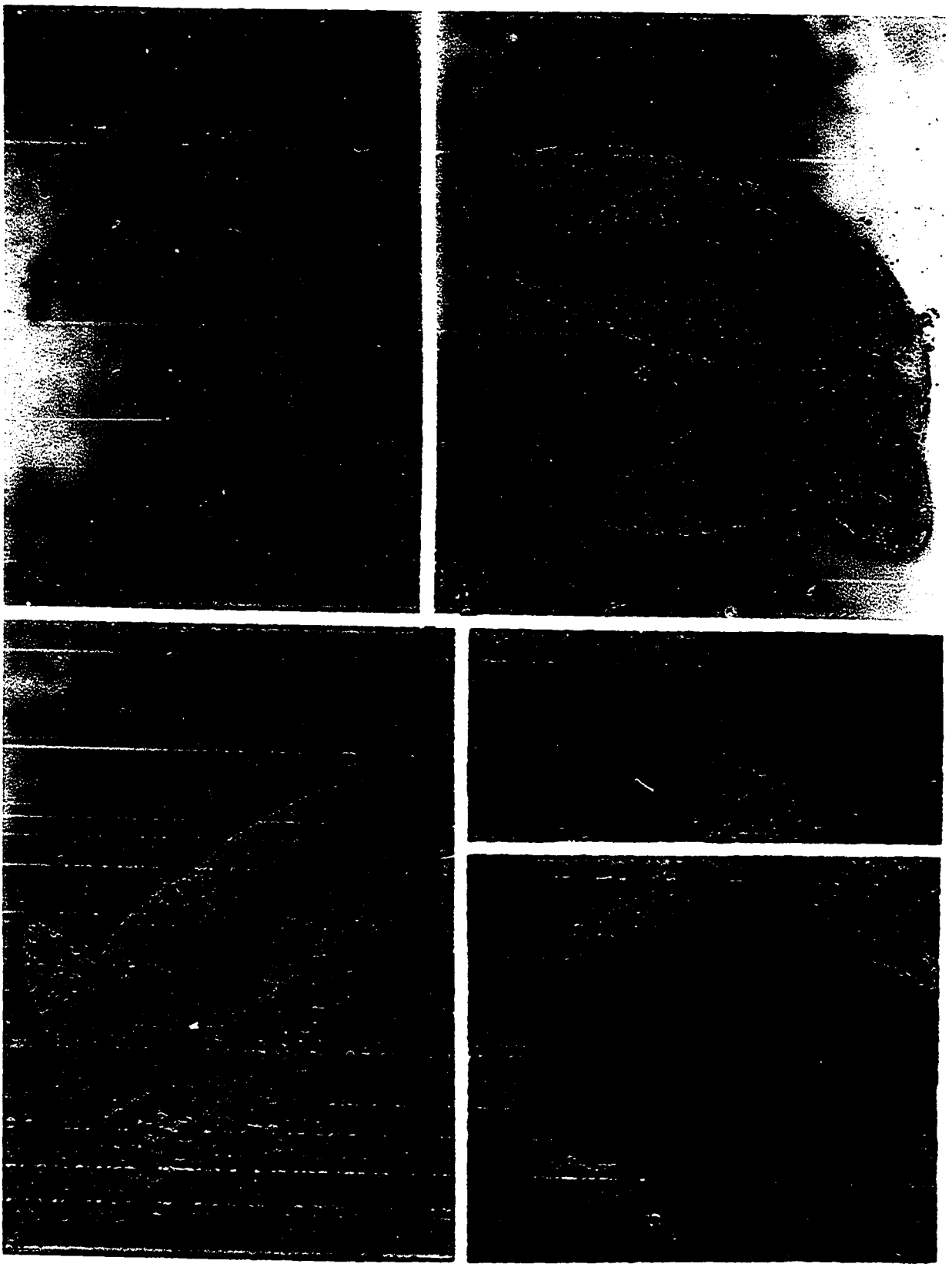


Plate VII

Fig. 36. C. vanelli miracidium attached by its terebratorium to H. trivolvis.

Fig. 37. C. vanelli redia emerging from attached miracidium. Note eyespot within the snail's tissues. (Same scale as in Fig. 36).

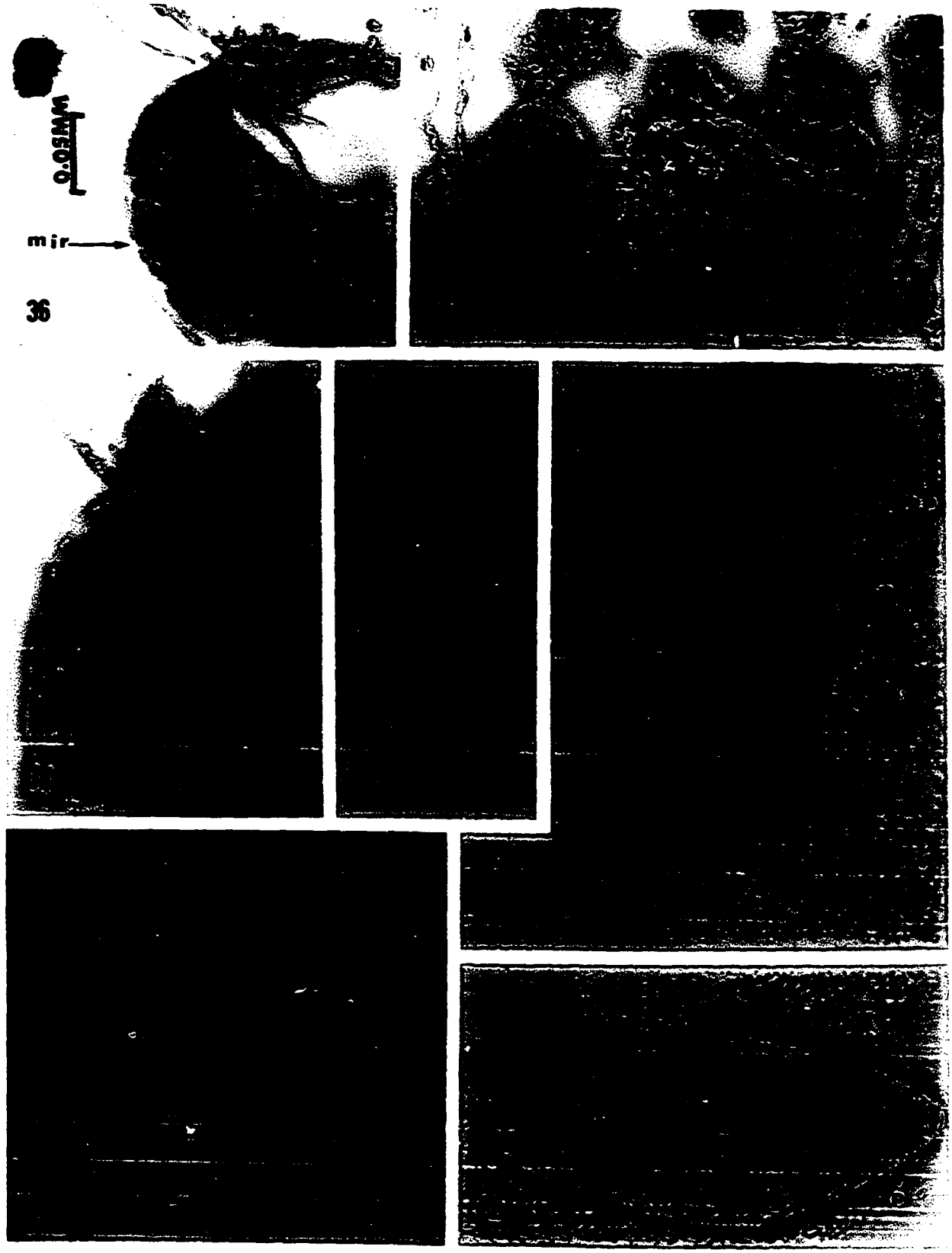
Fig. 38. C. vanelli redia almost completely within foot of H. trivolvis. Note empty miracidium. (Same scale as in Fig. 36).

Fig. 39. C. vanelli redia completely within H. trivolvis. (Same scale as in Fig. 36).

Fig. 40. Seven-day-old C. vanelli redia from G. hirsutus.

Fig. 41. Portion of C. vanelli redia from H. trivolvis 14 days post-exposure. Note birth pore. (Same scale as in Fig. 40).

Fig. 42. Twenty-one-day-old C. vanelli redia from P. gyrina. (Same scale as in Fig. 40).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